THE PHYSIOLOGY OF THE ELEPHANT

FRANCIS G. BENEDICT

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To Dr. Wm. M. Mann
with regards of
Francis G. Benedict

THE PHYSIOLOGY OF THE ELEPHANT

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THE PHYSIOLOGY OF THE ELEPHANT

INTRODUCTION[1]

Believing that the nutritional physiology of humans can be better interpreted by having available knowledge in comparative physiology, the Nutrition Laboratory has supplemented its major study of human physiology for the past three decades by a comparative study of the metabolism of animals of different species. Among the cold-blooded the observations have included large reptiles; and among the warm-blooded, animals varying in size from the 20-gram mouse to the 700-kg. Percheron horse and birds as small as the 20-gram canary and as large as the 17-kg. cassowary. Although the range in the body weights of these animals is great, the survey did not include the largest available warm-blooded animal. In comparative physiology, however, no comparison is complete unless the smallest and the largest animals of any given group are studied. The smallest available mammal is the 20-gram mouse, and the largest mammal other than the whale is the elephant, having a possible weight of more than 5000 kg.

Owing to the fact that it is the smallest mammal, extensive studies on the mouse have been deemed important. This animal is possessed of a peculiar metabolism in that it has a strong tendency to become at least semi-poikilothermic. The measurements on the mouse, therefore, partially tie in the warm-blooded series of animals with the cold-blooded series. The elephant, because it is the largest terrestrial warm-blooded animal, is just as necessary to the picture as the mouse. The elephant is several times as large as the next largest available mammal, that is, the fattened steer or the Percheron or Clydesdale horse. To attempt to predict the probable metabolism of an animal of 5000 kg. from measurements on an animal weighing only about 750 kg. is questionable, as are all extrapolations. From the standpoint of size alone, therefore, the study of mammals, to be complete, should include an investigation on the physiology, particularly the food and the metabolism, of the elephant.

The question naturally arises as to whether the elephant, because of its massive size, will show any striking difference in its metabolism from that of other warm-blooded animals, with particular reference to thermogenesis and thermolysis, heat insulation, and heat regulation. Thus, as regards the problem of energy transformations alone, the question naturally arises as to how these great creatures compare in their energy requirements with smaller warm-blooded animals. Are their energy needs in proportion to their weight or to their surface area or to some other function or factor, the blood volume, for example, or perhaps the heart rate or the blood pressure? All these and similar questions suggest themselves when one thinks of the elephant.

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[1] This study in its entirety could not have been consummated without the indefatigable efforts of Mr. Robert C. Lee of the Nutrition Laboratory staff. Practically every phase of the research profited by his superior technique and excellent judgment. The Misses Agnes G. Harrington and Helen G. Bulson were most effectively associated with the studies at Bangor, Maine, and St. Stephen, New Brunswick. The preparation of this report has had the supervision of the Nutrition Laboratory editor, Miss Elsie A. Wilson.

The value of knowledge regarding the physiology of the larger animals has been emphasized by the various, for the most part futile, attempts of writers to speculate upon this physiology. Pütter [1] in his interesting studies in comparative physiology stresses the desirability of information regarding the metabolism of the elephant and the whale, and reports a number of debatable calculations for these animals. Rubner [2] also, in his comparisons of the metabolism of different animals, speculates as to the probable heat production of both the elephant and the whale. In recent years there has been an increased interest in the metabolism and the physiology of the whale, and the absence of any accurate information regarding these points has led to an extensive series of calculations in attempts to estimate the body weight and the probable metabolism.[3] Of these two animals, the elephant and the whale, only the elephant is available for accurate physiological observations. One of the determining factors resulting in our study of the elephant, therefore, was the desirability of filling in the wide gap between the largest mammals heretofore measured and the largest available warm-blooded animal.

Early in our interspecific study of metabolism it was frequently found that knowledge of the physiology of one animal throws light upon the physiology of other animals. Since the elephant is so far removed in size from any other species, it seemed likely that findings on the elephant would be of unusual significance in interpreting earlier observations on other animals. Conversely, the physiology of the elephant should be illuminated by the investigations already carried out, for example, on the steer, the horse, and the sheep. Thus, although the elephant is a herbivore, its digestive tract is different from that of other Herbivora, such as the steer and the horse. Enormous quantities of food pass through its alimentary tract, and it is conceivable that the length of stay of the food in the alimentary tract and the accompanying chemical transformations and absorptions may not be the same as in the case of these other animals. The elephant is, therefore, of interest in comparison with other herbivorous animals and similarly with carnivorous and omnivorous animals.

In the Nutrition Laboratory's experimental program the effort has been made to combine purely physiological studies with observations that may be of value in other fields of science. For example, a recent survey of the food of the Maya Indians of Yucatan [4] was made not simply to record the food habits of the present-day Maya but likewise to determine, if possible, what these people ate in earlier times, with the view of supplementing other archæological findings. Similarly in our abstract physiological studies on large ruminants[1] valuable information was secured that is of assistance in the economics of feeding these animals. Since the elephant plays an important rôle in comparative anatomy and particularly in palæontology, it is surprising that modern studies of this animal have not been demanded by palæontologists, as they are always trying to trace the life of the ancient by means of observations on modern life, working forward from the fossil to the living animal and looking in fossils for indications of anatomical features present in animals today. Thus no feature of the study of the prehistoric elephant is any more emphasized than its wide geographical distribution. This would indicate that the prehistoric animal had great powers of adaptation, and the question arises as to whether this is also true of the modern elephant and whether it is any truer of the elephant than of any other large mammal. Hence an adequate scientific study of the modern elephant could not but help in palæontological findings. Merriam,[2] in discussing early man in America, states that recent palæontological discoveries in New Mexico leave no doubt regarding association of artifacts with remains of the elephant, and he emphasizes that in the next stages of advance in the study of early man in America, coordination of effort on the part of palæontologists, archæologists, and geologists is essential to integrate effectively all parts of the story so as to obtain the largest value from each phase of the investigation. This same coordination of effort is important in the study of the elephant. Such study should not be confined to anatomy. The feeding habits and the food with relation to structure should be investigated. In fact, there is an enormous field to be studied, both with the prehistoric and with the modern elephant, and a study of each type should throw light upon the anatomy, physiology, and life habits of the elephant.

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[1] Pütter, A., Arch. f. d. ges. Physiol., 1918, **172**, p 367; *idem,* Zool. Jahrb., Abt. f. allg. Zool. u. Physiol., 1923, **40**, p. 217.

[2] Rubner, M., Biochem. Zeitschr., 1924, **148**, p. 240.

[3] Guldberg, G., *Ueber das Verfahren bei Berechnung des Rauminhaltes und Gewichtes der grossen Waltiere,* Forhandlinger Videnskabs-Selskabet, Christiania, 1907, No. 3; Laurie, A. H., *Some aspects of respiration in blue and fin whales, Discovery* Reports, 1933, **7**, p. 363; Krogh, A., Nature, 1934, **133**, p. 635; Barcroft, J., *Features in the architecture of physiological function,* Cambridge, 1934, p. 121.

[4] Benedict, F. G., and M. Steggerda, Carnegie Inst. Wash. Pub. No. 456, Contribution No. 18, 1936.

As Miall and Greenwood[3] have pointed out—

> "Whenever the comparative anatomy of mammalia shall be exhaustively treated, the structure of the existing species of elephants will claim a principal share of attention. . . . Hence arise some curious physiological and mechanical questions to the student of elephant anatomy. What are the special modifications implied by a weight of perhaps three tons?[4] How nearly do the existing species approach the limits of size fixed by mechanical laws and by the physical properties of animal tissues? It would be an interesting task to investigate such problems as these, and to discuss the many points of anatomy, morphology, physiology, and palæontology suggested by the examination of a dead elephant."

If knowledge regarding the *dead* elephant will contribute so much to science as a whole, how much more substantial a contribution can be expected from a study of the vital processes of the *living* elephant!

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[1] Benedict, F. G., and E. G. Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, and Pub. No. 377, 1927.

[2] Merriam, J. C., Report of XVI International Geological Congress, Carnegie Inst. Wash., News Service Bull., 1935, 3, No. 23, p. 185.

[3] Miall, L. C., and F. Greenwood, Studies in Comparative Anatomy, No. II, *Anatomy of the Indian Elephant,* London, 1878, p. 5.

[4] There have actually been elephants weighing twice three tons, notably Bolivar (see pages 108-109).

Observations on the elephant as it exists today are, therefore, of interest from at least four standpoints—comparative anatomy, palæontology, the physiology of the elephant *per se,* and comparative physiology. Furthermore, it is not impossible that an abstract study of the physiology of the elephant may prove of real practical value in suggesting betterments in the hygiene and care of this animal in captivity. A study of the elephant was, therefore, undertaken by the Nutrition Laboratory, with emphasis placed upon its nutritional physiology. The pathology of the elephant did not enter into our program. Pathological studies are useful in interpreting and supplementing physiological investigations. This is especially true of human pathology as associated with human physiology. But the pathology of animals as a whole, save for the domestic animals, is at present almost an unexplored field. As concerns domestic animals, the economic importance of knowledge of animal pathology can not be overestimated. Little progress in animal pathology can be made, however, until a fundamental knowledge of animal physiology has been acquired. Hence emphasis is placed in this report upon the physiology rather than the pathology of the elephant.

During our collection of data on the elephant and the preparation of the results for publication, a number of zoologists and practical animal men urgently requested that the material be presented in such a way as to be of use to them as well as to specialists in the field of physiology. Consequently, although stress has been laid upon the physiology of the elephant, this report has not been written exclusively from the standpoint of pure physiology but has been prepared with the idea of making it useful in other fields as well. The legends and fantastic speculations that are so plentiful concerning the elephant (even as early as the time of the elder Pliny [1]) will necessarily be referred to occasionally, especially in consideration of literature already published on the elephant, but every attempt will be made to distinguish between legends and attested facts, with the emphasis always upon attested facts and with the zoologist, practical animal man, and palæontologist in mind as well as the physiologist.

EARLIER OBSERVATIONS ON THE ELEPHANT

For obvious reasons the two largest living mammals, the whale and the elephant, have been until recently studied only inadequately. Fossil whales and fossil elephants have received an unusual amount of attention from palæontologists, and our knowledge of these animals is continually increasing. The studies of Remington Kellogg [2] particularly have thrown much light upon the prehistoric whale and its transition from a land to a water animal. Fossil studies of the elephant have likewise given much information regarding its nature, its feeding, and its geographic distribution. For our present-day knowledge of the prehistoric elephant, we are indebted to the late Henry Fairfield Osborn and his colleagues.[1] Chaney [2] has considered the probable feeding habits and food supplies of the shovel-tuskers (Amebelodontinæ). This animal has been traced from its probable original habitat in Africa through Asia into America and the states of Kansas and California. In late Tertiary deposits in Turkestan there have been found remains of roots, stems, and leaves of pond-lilies and other aquatic plants. The occurrence of these plant fossils in beds of the same age as those containing the shovel-tuskers, on both sides of the Pacific, suggests a swamp habit of feeding for these peculiar animals. The living moose eats similar food over much of its range. The Proboscidea in general have always challenged attention, and interest in these prehistoric animals was stimulated by the finding of nearly intact mammoths in the glaciers of Siberia.[3] Knowledge with regard to the modern elephant, however, is much more meager than is knowledge of the prehistoric elephant.

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[1] For Pliny's account of the python and the elephant see page 236.

[2] Kellogg, R., Carnegie Inst. Wash. Pub. No. 346, 1927, and Pub. No. 348, 1920, and Pub. No. 447, 1934.

The elephant today is found in four environments: (1) In the wild in Asia and Africa; (2) in captivity, where it is much used for labor and hunting, especially in India; (3) in zoological gardens where it becomes accustomed to long confinement under one environment and one regime of living; and (4) in the traveling circuses with menageries, particularly in the United States and in Europe. Usually elephants are a featured part of such menageries, and these circus elephants, particularly the larger herds, are of special physiological interest, inasmuch as they must adjust themselves rapidly to a change in environment almost daily in their travels to and from different cities and parts of the country.

In the wild state the elephant has always presented great attraction for the hunters of big game and of ivory. In India the elephant is employed today in tiger hunts, a usage that rarely does harm to the animal. But in Africa the elephant is hunted for itself. The specimens secured for well-ordered museums are permissible, but a large number of elephants are killed for sport to secure as trophies the head and the tusks. The tremendous demand for ivory has resulted in inroads both by natives and professional ivory hunters on the elephant herds in Africa, which have been so ruthlessly destroyed that governmental protection in the form of preserves is now necessary.

The elephant has long been captured for domestic uses in India and more recently in Africa. The result is that much has been written regarding these phases of elephant life, with observations frequently as diverse as the number of writers. The literature with regard to the elephant in captivity in India and Africa deals, for the most part, with its use as a beast of burden and for military service. In much of the earlier literature, in novels, and in poetry we find detailed accounts of the military use of the elephant by the ancients, especially in the classic references to

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[1] Osborn, H. F., ***Proboscidea. A monograph of the discovery, evolution, migration and extinction of the mastodonts and elephants of the world.*** In press; idem, Proc. Nat. Acad. Sci., 1935, **21**, p. 404.

[2] Chaney, R. W., *The Kucha Flora in relation to the physical conditions in Central Asia during the late tertiary,* Svenska Sällskapet för Antropologi och Geografi, Geografiska Annaler, 1935, Sven Hedin, Arg. XVII, p. 92; *The food of fossil elephants,* Carnegie Inst. Wash. News Service Bull., 1935, 3, No. 22, p. 177.

[3] Digby, B., *The mammoth and mammoth-hunting in North-East Siberia,* New York, 1926.

Hannibal's employment of African elephants in crossing the Alps.[1] The impressive size of the elephant was valuable in striking terror upon the enemy who had not become acquainted with it. Its height furnished an advantage in attacks upon the enemy, and its strength was utilized in transporting the baggage and military accoutrement during campaigns. In many accounts of military combats, big-game hunting, and ivory hunting, however, there is little of any scientific value, and hence this type of literature is of no interest in this monograph.

Concerning the elephants living in zoological gardens the literature contains a variety of comments, most of them consisting of superficial observations on growth and size and occasionally fragmentary reports of a partial necropsy. (See page 108.) Emphasis is sometimes laid upon the pathology, but there has been no systematic study of the physiology of the elephant. Those papers that are scientific rather than popular, however, are published in general in zoological society reports, especially from the splendid gardens in London, Hamburg, New York, and Philadelphia. So far as this type of literature goes, it is of real value. But it is limited and widely scattered, since the papers appear usually in zoological society reports that are purely local in publication, difficult for the average reader to secure, and too frequently not cited by other writers.

The literature on the elephants in circuses consists almost exclusively of popular exploitation of the alleged prowess, memory, strength, fidelity to keeper, and antipathies of the animal, portrayed usually with the proverbial distortion and romancing which is assumed to be the inalienable right of circus advertising men and writers of circus stories. Yet the debt due to the circus is great. For example, the finest herd outside of Asia or Africa today is that of the thirty-four elephants in the Ringling Brothers Circus, a herd with which millions of young Americans have been brought in direct contact. The circus brings to thousands of communities, that are not able to afford a zoological garden, specimens of this noble animal for countless numbers of children and adults to see at first hand, an experience far more convincing and resulting in information more permanently retained than our modern motion picture projections of elephant life in the wild. These usually show fear and flight most strikingly, but little of normal, reposeful forest life. Such films do, however, convey much important information and are greatly to be desired as permanent records, before the ravages of the hunter drive these animals more and more into special compounds. In fact, the motion pictures showing the habits of the animal in the wild are a real contribution to what might be termed the ecology of the elephant.

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[1] This military exploit has intrigued many historians, and a number of volumes have been written on it. Typical of these is the book of John Whitaker entitled *The Course of Hannibal Over the Alps Ascertained,* published in two volumes in London, 1794. This book is a strange combination of most elaborate literature citations and emphatic personal opinions. Although it is generally believed today that without doubt Hannibal used African elephants, Whitaker says that the historian Polybius states that Hannibal had Indian elephants. The number of elephants, thirty-seven, seems to be well established, however. Whitaker emphasizes perhaps more than any other writer the fact that the elephants had a shortage of food, for he states that the elephants were starving all the while. There was grass upon the ground, but it was buried under snow. Perhaps no one feature of Hannibal's campaign is any more puzzling than the question as to how he could have transported sufficient fodder for this herd of thirty-seven elephants. Many of them doubtless were lost. Indeed it has been proved that they were lost before the final descent into Italy. In his second volume (page 178) Whitaker also emphasizes the fact that the elephants had been transported from the warmth of their native clime and brought to encounter the blasts, snows, and frosts of the Alps. They were thus reduced to great distress. Whitaker, like all the earlier historians, had to rely almost exclusively upon the writings of Livy and Polybius.

In this memoir there is no pretense to a complete compilation of the literature on the elephant, but emphasis has been laid, first, upon securing all the physiological data available and, second, upon those observations concerning the acclimatization of the elephant, the tendency of the animal to stampede, its nervousness, and particularly its nutrition.

Aristotle (B. C. 384–322)—The earliest suggestion of a scientific study of the elephant is that referred to in a letter by Dr. William Ogle, published by Miall and Greenwood,[1] as follows:

> "Aristotle most probably, as I think, never saw an elephant himself, but the following passages from his *Historia Animalium* show that even at that early time some one or other either had or professed to have examined the inside of one.
>
> "II. 17. 'The elephant's intestine is formed of parts so put together as to give the appearance of there being four stomachs. Its viscera resemble those of the hog, but are of course much larger. The liver, for instance, is four times as large as that of an ox. The spleen, however, is of small size, considering the large bulk of the animal.'
>
> "II. 1. 'The penis of the elephant is like that of the horse, but small considering the animal's bulk. The testes are not visible, externally, but are placed inside, near the kidneys. The pudendum of the female is placed in the position which in ewes is occupied by the dugs, but for congress is drawn upwards and directed outwards, so as to facilitate the action of the male. It has naturally a wide orifice.' "

As Miall and Greenwood state, "the description of the generative organs seems to imply actual dissection by some ancient anatomist."

Galen[2] (A. D. 130–200?)—The first authoritative, recorded dissection of an elephant that can be definitely ascribed to a known individual was that made by Galen some five hundred years after the time of Aristotle. Dean George D. Chase, of the University of Maine, has kindly translated for us paragraphs from the Latin translation of the works of this Greek physician and medical writer, showing that Galen had intimate contact with the dissection of an elephant and that he found a sclerotic condition of the heart, which he describes as a "bone of the heart."

Moulines[3] likewise apparently dissected an elephant that had been killed by fire in Dublin. Unfortunately his published report is inaccessible.

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[1] Miall, L. C., and F. Greenwood, Studies in comparative anatomy, No. II, *Anatomy of the Indian elephant*, London, 1878, p. 62.

[2] Galen, C., Latin translation of Galen's works, Lyons, 1550, I, p. 295. (De Anatomicus administrationibus, Book 7.) That Galen was apparently much interested in the elephant in general is evidenced by some dozen or more of the titles of his articles. (See page 297.)

[3] Moulines, A., *An anatomical account of the elephant accidentally burnt in Dublin on Fryday, June 17, in the year 1681*, etc., 1682.

Hartenfels[1]—Of the literature other than that dealing exclusively with the anatomy of the elephant, the earliest that we have selected for discussion is the singular book of Hartenfels. Thanks to the kindness of Professor C. A. Kofoid of the University of California, we were permitted to borrow from his library both editions of this interesting book. Both editions deal with the general anatomy of the elephant, with special reference to the proboscis, the tusks, the teeth, and the digestive tract, and contain comments on its age, nutrition, capture, docility, and use in war and triumphal spectacles, in pageants, and religious observances. Hartenfels reports that he himself saw but one elephant and that the statements in his book are in large part quotations from others. He makes extensive citations of the earlier literature on all phases of elephant life, quoting from publications in all languages and making an indiscriminate choice of quotations, whether legend, fiction, or fact. Both editions of Hartenfels' book contain a number of interesting plates, but it would appear that the artist who drew the illustrations had had little direct acquaintance with the elephant. He probably had not seen the elephant that Hartenfels states he saw, for he depicts the proboscis as a series of spiral rings much like the well-known "horn of plenty." In these illustrations also the eyes are usually shown directly in front of the forehead instead of being on the side, and the ears are not like the ears characteristic either of the Indian or African elephant. However, they more nearly represent the Indian than the African form. The body is depicted as extremely fat, and in general bears only an approximate resemblance to either of the well-known types of elephant. An interesting quotation bearing on the sleeping habits of the animal states that when elephants become older, they can not bend their legs, and so when they sleep, they lean against trees. Hartenfels says this statement is false.

Armandi[2]—In the numerous references to the use of the elephant in war, in accounts of military history from 330 B. C. until recent dates, there are statements regarding physiological phases of this animal's life which have a definite bearing upon our own study. The most complete analysis of the use of the elephant in warfare is the carefully written treatise of Armandi, which contains particularly valuable résumés of the earlier historians' reports on the participation of the elephant in military affairs.[3] The first recorded use of elephants in war was in the battle of Arbela, fought between Alexander the Great and Darius in 331 B. C. These were Indian elephants, for it was not until the time of the Ptolemys that the African elephant began to appear. Prior to the development of firearms, these animals were extremely effective in warfare, although probably as much because of the terror inspired in the enemy by their unusual size and shape as because of the actual destruction by the animals themselves. In these military campaigns practically all the armies had herds of from thirty to one hundred or more elephants. Armandi confirms the belief that in earlier times the elephant certainly lived in Africa as far north as the Mediterranean, but that they were gradually driven south by their capture for military purposes and particularly by their slaughter for ivory. This expressed opinion gives us the first suggestion that the elephant may not have been as exclusively a tropical or equatorial animal as has been commonly believed.

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[1] Hartenfels, Georg. Christoph. Petri ab, Elephantographia curiosa, seu Elephanti Descriptio, juxta methodum et leges imperialis academiæ Leopoldino-Carolinæ naturæ curiosorum adornata, multisque selectis observationibus physicis, medicis et jucundis historiis referta, cum figuris aeneis. Erfordiæ, 1715. Typis Joh. Henrici Groschii. 284 pag. Idem. Edit. altera auctior et emendatior, cui accessit ejusdem auctoris oratio panegyrica de Elephantis, nec non Justi Lipsii epistola de eodem argumento erudite conscripta. Lipsiæ et Erfordiæ, 1723. Typis Joh. Mich. Funckii. 284 et 20 pag.

[2] Armandi, P., ***Histoire militaire des éléphants, depuis les temps les plus reculés jusqu'à l'introduction des armes à feu,*** Paris, 1843.

[3] See, also, the brief historical account of the use of the elephant in war by W. Stricker, Zool. Garten, 1878, **19**, p. 380.

Of the many campaigns described by Armandi, none is more interesting from the standpoint of physiology than that of Hannibal in his historical crossing of the Alps.[1] When he left Spain, he had forty elephants. When he crossed the Rhone, he still had thirty-seven, but in crossing the Alps he suffered a terrific loss. History does not tell how many. Armandi mentions that it is natural to suppose that shortage of food and the extreme cold had a very disastrous effect on the elephants, who were less able than the men and horses to travel through the snowy, icy routes. Some were saved, however, and took part in the battle of Trebia. Shortly thereafter, according to Polybius, Hannibal lost all his elephants, with one exception. The early historians point out that the loss of these animals was caused not only by the arms of the Romans but by the icy rain and sleet that fell during the action. Eight elephants survived the battle of Trebia, but seven perished in the Apennines the following spring. No matter how well these animals had adjusted themselves to the climate and to the cold, severe rigors of Hannibal's campaign, the fact that they perished so quickly is in full conformity with the present belief by keepers in parks and of elephant herds in general that the elephant has a low resistance to severe cold.

Owing to the tendency of the elephant to be frightened by unusual sounds, attempts were made by the enemy to disturb them by the use of firebrands and musical sounds. The squealing of a pig seemed to be particularly disastrous to the peace of mind of the elephant. Frequently the animals were more dangerous to their own armies than to those of the enemy, owing to their disposition to stampede. Following the introduction of firearms in countries where elephants were used, it soon became apparent that these animals were of little value in military service and actually often became the inevitable cause of a reverse. Consequently thereafter the use of the elephant as an instrument of warfare rapidly decreased.

The two features of physiological interest in this military history are the elephant's susceptibility to severe cold and its tendency to stampede and become unmanageable. All the Carthaginian elephants were African. The ears of the African elephant are approximately three times as large as the ears of the Indian elephant. One can readily believe, therefore, that in their passage of the Alps, where they had to pass through snow and over frosty ground, Hannibal's African elephants, in spite of any artificial covering, must have suffered greatly from their frozen ears and frozen trunk tips. That many were injured by accident in the deep defiles is undoubtedly true, and that many were lost by pneumonia or other respiratory infections because of the severe cold is highly probable, although not stated by the historians.[1] The nervousness and excitability of the elephant, resulting in stampedes, complete routing, and the loss of battles, as recorded in military history, is precisely what one would expect from the well-known habit of the elephant to become panic-stricken without any explanation and to stampede. No one factor in the life of the elephant is more guarded against by keepers than the possibility of their becoming frightened over a seemingly small occurrence.

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[1] Historians have laid great stress upon Hannibal's campaign and his use of elephants, but rarely does one see any comment regarding the crossing of the Alps by Hasdrubal, who is credited with having had fifteen elephants in his expedition.

The classical writers who have reported the use of elephants in war frequently have given the heights of the animals, but in none of these early reports, even in the survey of the classical military descriptions made by Armandi, does one find recorded the weights of the animals. Suitable apparatus was probably not available for weighing the equivalent of three or four tons. The Romans, to be sure, used the balance for weighing smaller objects and the steelyard for heavier ones, but it is believed always with a single beam.

Mayer [2]—One of the numerous early anatomical studies is that reported by Mayer. He emphasized the extraordinarily small throat of the elephant and inferred that the animal can eat only very small mouthfuls of completely comminuted food. The error of this inference that the food is completely comminuted will be shown subsequently. (See page 169.) Mayer made his measurements on a female elephant, the total length of the intestines of which he gives as 75 feet (23 meters).

Gilchrist [3]—The first authoritative, practical discussion of the elephant was that published in 1851 by Gilchrist. Devoted in large part to considerations of the pathology of the elephant and of various other animals, much of his material was evidently used later in the book of Evans. (See page 11.) Gilchrist states that many observations on the heart rate of the elephant show that the average, healthy pulsation of the heart is 49 beats per minute. The pulse rate may increase to from 90 to 100 beats per minute, but the heart is probably smaller than in the other large quadrupeds. Drinking water was given twice a day, 15½ gallons at a time. No urine analyses were made. Particular reference to Gilchrist's extraordinarily complete dissection of the elephant is made on page 108 of this report.

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[1] Dr. Ludwig Zukowsky, of the Carl Hagenbeck Tierpark, Germany, points out (in personal correspondence) that the Carthaginians may have protected the ears of the elephants against the cold in the higher regions of the Alps. He believes that in the Middle Ages men knew more about the care of animals than they do now, as evidenced by the fact that it was possible in Nero's time to capture and maintain five hundred lions and that adult African male elephants (today a wonder in captivity) were at that time found in Rome in dozens. How the Romans and Carthaginians captured and maintained these giant animals is a riddle. Probably all these elephants came from the valleys of the Atlas mountains, and perhaps Hannibal captured his elephants there, for in Spain there were no elephants in those days.

[2] Mayer, C., *Beiträge zur Anatomie des Elephanten und der übrigen Pachydermen,* Nova Acta Phys.-Med. Akad. Caes. Leop., Halle, 1847, 22, pp. 30 *et seq.*

[3] Gilchrist, W., *A practical treatise on the treatment of the diseases of the elephant, camel, and horned cattle, with instructions for preserving their efficiency,* Calcutta, 1851.

Watson [1] discusses the regurgitation of water in the throat and the sucking power of the trunk to pull up water. Of interest in our study, with special reference to the possibility of air being passed through the mouth, is Watson's statement that—

"The formation of the mouth of the elephant, however, is such as to prevent the trunk ever being grasped by the lips so as effectually to stop the entrance of air into the cavity."

Miall and Greenwood [2]—In their study of the anatomy of the Indian elephant, these authors place emphasis upon the slow alteration in the food as it passes through the alimentary tract of the elephant. They say that "even in the large intestine the original form of many pieces of vegetable food is retained, and grains of maize were recognizable in the colon of our example, as were hay and potatoes in the colon of that dissected by Camper." [3] Miall and Greenwood are not certain, however, that these appearances of food were not due to disease. In their general classification of the principal memoirs on the anatomy of the elephant, Miall and Greenwood give an extensive list of titles, many of which have been incorporated in our Bibliography on pages 293 to 300.

Evans [4]—The notable work of Evans is probably the most authoritative study on the elephant, the most outstanding from the standpoint of scientific literature, and the most comprehensive. The book was written in India, with the main object of making it of practical use. It, therefore, deals exclusively with the Indian elephant, with no discussion of experiences with African elephants, with feeds other than Indian feeds, or comments on the animal's adjustment to a new climate and new environment. The book is almost inaccessible in the United States and only rarely can a copy be found. It contains a large mass of material collected from the earlier writers and also a vast amount of information based on his own personal experiences. The sleeping habits, the feeding with extensive use of a native grass called "Kiang," the allowance of about 2 ounces (57 grams) of salt per day, and the importance of drinking water are subjects of considerable discussion in Evans's book. His mention of sweat glands is of special interest in connection with our study of heat regulation and water of vaporization. The secretion of sweat is so small that it is best seen only after the removal of pack gear. Fever, the use of the clinical thermometer, and the significance of slight rises in body temperature are considered from the standpoint of hygiene. This most interesting book is imbued with the viewpoint of the veterinarian, having in mind the health and welfare of large herds of animals. Some of the statements by Evans are so at variance with our own experience as to lead us to believe that they apply only to the local conditions in India.

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[1] Watson, M., Journ. Anat. and Physiol., 1874, **8** (2d ser., **7**), p. 90.

[2] Miall, L. C., and F. Greenwood, Studies in comparative anatomy, II, *Anatomy of the Indian elephant,* London, 1878, p. 57; idem, Journ. Anat. and Physiol., London, 1877-78, **12**, pp. 261 and 385; *ibid.,* 1878-9, **13**, p. 17.

[3] Camper, P., *Description anatomique d'un éléphant mâle,* Publiée par son fils, A. G. Camper, Paris, 1802.

[4] Evans, G. H., *Elephants and their diseases,* Rangoon, 1901 and 1910.

Sunamoto [1]—An exceptionally comprehensive compilation of the literature on the elephant, dealing with the anatomy and natural history, the habits, the legends, and the ivory of the elephant and including much of what little has been already reported on its physiology, has been published by Sunamoto. The material is in two volumes, each over one thousand pages in length. The text matter is written in Japanese, contains a 102-page subject index in Japanese, and is plentifully illustrated. There is also a 16-page table of contents in English and a bibliography in English comprising 1069 titles. Sections of Sunamoto's text that deal more particularly with the problems of interest in this monograph were kindly translated for us by Mr. S. Shimoyama, assistant in the Japanese-Chinese Library at Harvard University, where the books are on file. Some of the references cited by Sunamoto are listed in our Bibliography, but with many of his citations we have not got in touch. Any one interested especially in the anatomy, the folklore, or ivories of the elephant should most certainly consult Sunamoto's books.

Summary regarding the literature—Much of the fairly large amount of published material with regard to the modern elephant represents erroneous statements, fantastic notions, and legends which have been handed down from writer to writer. The main object of such literature is to keep fresh old stories and legends and to keep up popular interest in the elephant. A great deal of the literature likewise is confined to the military use of the Indian elephant, its capture, its use in hunting for ivory and for sport. There is little that can be classified as scientific literature, and in the field of physiology there is almost nothing. Most of what is of value has been collected by Evans. Statements with regard to the heart rate and the respiration rate occasionally appear, but for the most part there is a great dearth of authentic information. The study of the anatomy of the elephant has been the most extensive. Indeed, the scientifically important titles in the literature deal for the most part with the anatomy. These reports were stimulated without doubt by the massive size of the elephant and the relative rarity with which the elephant could be studied. But notwithstanding the century or more that has passed since the first anatomical studies of the elephant, there are still problems that need to be settled in this field in order to interpret adequately some of the present-day physiological findings. For example, further information is needed regarding the anatomy of the respiratory tract, to classify knowledge regarding the elephant's breathing habits. The general digest of the literature presented in the immediately preceding pages is by no means to be taken as inappreciative of the numerous smaller contributions made from time to time during the last century. These will be referred to in detail in later parts of this monograph. The main thought in digesting the earlier literature on the elephant, both in this section of the report and in later sections, has been to select from the vast amount of written material those statements that may be termed "attested facts," and to disregard, except in rare instances (and those especially labeled) the legendary tales concerning these curious animals. The citations made in this report of articles dealing with the elephant, particularly its physiology, are summarized in the Bibliography. In the search for physiological data on the elephant many titles have been unearthed, especially dealing with the anatomy of this animal. Of these titles mention will be made in the subsequent pages only of those that have special bearing upon the numerous physiological problems that will be emphasized. To aid other investigators who may be interested in the literature on the elephant from the anatomical and other standpoints, many other references that have been found and that are not cited on the following pages have been listed in a supplementary bibliography at the end of this report.

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[1] Sunamoto, E., *The elephant,* Osaka, 1931-32.

PLAN OF RESEARCH

To conduct a physiological study of the elephant comparable in extent and accuracy to the investigations made by the Nutrition Laboratory on other animals, both cold-blooded and warm-blooded, necessitated most careful experimental plans. We were interested primarily in studying the gaseous metabolism of the elephant. This type of study calls for more than ocular observations made while one sits in a chair in a zoological park or feeds peanuts to circus elephants. Measurement of the metabolism or heat production of an animal of such huge size presents a unique problem, bringing into play more nearly engineering than physiological skill. This realization, together with the knowledge of the time, labor, and expense necessary in obtaining such measurements and the natural disinclination of elephant owners to permit any "experiments" on animals that are so costly, made an attack on the problem seem almost impossible. Since 1910, however, the thought of measuring the elephant's metabolism has been under our consideration. Direct, personal observations of elephants were made during these many years at several zoological parks, particularly in New York City, in Washington, D. C., and in Philadelphia. When studying large cold-blooded animals at the New York Zoological Park, we spent many hours with the several elephants there, making calculations as to the possibility of determining the heat production of these great creatures. Again in more recent years observations were made at this same Park, where the Director, Dr. W. Reid Blair, and Dr. Raymond L. Ditmars and Dr. C. V. Noback gave every possible encouragement. In addition, advantage was taken of the opportunity of observing the elephants at the animal farm of Mr. John T. Benson at Nashua, New Hampshire. These personal observations, along with many hours of conversation and observation with Dr. Ludwig Zukowsky and Messrs. Heinrich and Lorenz Hagenbeck and contacts with theatrical agencies, continued throughout many years. The hope was always entertained that favorable conditions for studying the elephant might present themselves. It was realized that chance observations of a day or two on any elephant that might happen to be brought into town would be of no value, but that for the best contribution to the physiology of the elephant as many kinds of observation as possible should be made simultaneously upon the same animal. An experimental plan comparable in extent and details to those already carried out by the Nutrition Laboratory on other species of animals was, therefore, early decided upon, and the delay in actively prosecuting the research was due solely to inability to secure a suitable elephant. Finally in the spring of 1935 opportunity was offered to study a fine specimen of the elephant in considerable detail. The important findings and unusual features that appeared in this first concentrated study were later supplemented by more general observations on three herds of circus elephants and three zoological park elephants.

Plans were made for securing all those gross observations that can be made on an animal without particularly complicated appliances, such as records of the body weight, body height, length, and girths, respiration rate, habits of eating, and digestibility of food. Study of this latter factor included recording of the weights of intake of both feed and water and the weights of outgo of feces and urine during a 9-day period. Records were made of the time and frequency of passing feces, comparison of the feces temperatures during the day and night, weights of individual defecations and of individual boluses, linear measurements of the largest bolus, color, odor, and other general characteristics that can be noted from a macroscopic examination. The stimuli to defecation, such as standing up on the hind legs prior to circus performances, were also noted. Similarly, observations were made regarding the frequency of discharge of urine, the time of voiding, the amount of each urination, comparison of urine temperatures during the day and night, comparison of urine and feces temperatures, study of the stimuli to urination, and preliminary movements prior to urination. The frequency of drinking water, the amounts drunk, and the temperature of the water were noted. Activity records, which are of special interest in comparative metabolism studies, included an analysis of the habits of the elephant when standing, the degree of motion of the main part of the body itself, and of the head, trunk, ears, tail, and legs, records of the length of time spent lying, the frequency of change of body position, the time of night when the elephant lies down, the sleeping habits, the "nesting" habits, and any phonations or sounds. In a special study of mouth versus trunk breathing the effect of closing the end of the proboscis was noted. All these records may be termed superficial observations, which can be made without special apparatus. For these studies elephants could be used that were not strictly confined. Many such observations could have been made long ago in zoological parks or circuses, and it is surprising that they have not.

The more exact measurements of the internal processes of the animal organism require larger, more complicated equipment, and our main efforts were directed toward the securing of such types of observation. The food of one elephant was subjected to chemical analysis for water, nitrogen, crude fiber, fat, chloride, and ash content, and for heat of combustion. The feces of this same elephant underwent similar analyses for the purposes of comparing the composition of the feces with that of the food. The feces of nine other animals were likewise analyzed chemically, and microscopic examinations of the feces for parasites were made in many instances. Chemical analyses of the urine gave information regarding the specific gravity and the total nitrogen, ammonia, urea, creatine, creatinine, allantoin, total sulphur, and chlorides. Microscopic analyses of the urine included a search for blood, pus, casts, and bacteria. Observations were also made of the specific gravity, the reaction, and the presence or absence of albumin, diacetic acid, bile, and sediment. The rapidity of passage of food through the intestinal tract was studied by means of rubber bands given with the food. Chemical analyses of the drinking water of one elephant were made for information regarding total solids, total mineral residue, and total chlorine. In addition to the temperature measurements of feces, urine, and drinking water, measurements were made of the body temperature (temperature of the skin, particularly on the ear, and temperature of expired air) and the temperature of the environment (barn and respiration chamber). An especially important study was that of the heart rate.

The most complicated and unique measurement was that of the total energy production or the total metabolism. This necessitated a respiration chamber for a study of the respiratory gases (carbon-dioxide production, oxygen consumption, respiratory quotient, methane production, and water vapor output), since direct calorimetry was out of the question. A complete digestion experiment with an energy balance could have been attempted without a respiration chamber. But since the use of a suitable elephant was secured for a fairly long period, the time obviously was ripe for a comprehensive study of the gaseous metabolism. Because of the particular respiratory mechanism associated with the trunk of the elephant and because of the belief of many individuals that the elephant can breathe only through the trunk, the gaseous exchange from the trunk alone was likewise measured for comparison with the measurements of the products of respiration from the entire body.

ELEPHANTS STUDIED

CAPTIVE VERSUS WILD ANIMALS

Ideally animal studies should be made upon animals taken directly from the wild, for apparently the wild animal may have a somewhat different metabolism from that of the domesticated animal. The wild rat, for example, has a measurably higher metabolism than the laboratory-bred albino rat.[1] It is seldom practical and usually impossible to study wild animals. Indeed, most of the animals upon which the Nutrition Laboratory has made metabolism measurements had been for some time previously or all their lives in captivity, and as a most important reason for studying the elephant was to compare it with the other animals that had been measured, we believed that it should be living under conditions comparable to those under which these others were studied. It may be argued that the elephant subjugated to the qualitative and quantitative restrictions of man has a daily life entirely different from that of the elephant in the wild, and that observations made upon the captive animal would have little true physiological value. Only gross observations of animals in the wild can be made, however, and observations on the heart rate, the respiration rate, the urine, and the metabolism are impossible. Various writers, especially hunters, have commented upon the feeding habits of wild animals, based upon the study of the destruction of plants, possibly the crude inspection of the feces, the migrations of the animals, the diurnal variations in activity, and the like. Usually these observations concern experiences with animals not in the repose of their normal daily life but in flight or subjected to fear, just as are the extraordinary motion pictures of animals that have been presented to the American public in the last few years. Many observations of elephants have been made during the process of capture, as they were being driven into an enclosure. But the behavior of a newly captured wild elephant reflects tremendous tension and the psychology of fright. Consequently such studies are of little physiological value, and we must for this reason also resort to a study of animals accustomed to long-time captivity.

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[1] Benedict, F. G., and J. M. Petřík, Amer. Journ. Physiol., 1930, **94**, p. 662; Benedict, F. G., and E. L. Fox, Amer. Journ. Physiol., 1934, **108**, p. 285.

No one has given more intelligent thought to the handling of captive animals in zoological gardens than has Dr. W. T. Hornaday, Director Emeritus of the New York Zoological Park, who has pointed out that in captivity animals enjoy many advantages. Among these is the absence of enemies. In the wild, animals are constantly fighting for their lives, although this probably is not true of the elephant. Furthermore, if they are quarrelsome and dangerous, captive animals can be separated from each other so that no fighting takes place. Rarely is there a shortage of food, at least so far as quantity is concerned, especially in well-organized zoological gardens. Wild elephants are invariably infested with parasites, whereas practically all elephants in circuses and zoological parks can be kept free from such pests by intelligent keepers. Dr. Hornaday believes that animals in captivity have a much easier life and probably live as long as, if not longer than, animals in the wild. On the other hand, the food is selected by man, is, therefore, artificial in nature, and there is always the question whether captive animals receive sufficient vitamines and salts, which undoubtedly animals in the wild find by instinct in herbs or other foods that furnish medicinal needs. The modern experience of feeding not only infants but animals, however, with emphasis upon the importance of salts, vitamines, and ultraviolet light, has changed considerably the technique and the success of breeding and raising animals in zoological parks. Thus, whereas formerly park-born animals for the most part suffered from illnesses, especially rickets, now they are raised in perfect health and apparently, save for the lack of optimum exercise,[1] are equal physically to those born in the wild.

That life in captivity has not been to the detriment of animal health is shown by the improvement in many species of animals resulting from the cross-breeding by man. The modern productive hen has been developed from the jungle fowl, and cattle have been highly improved by breeding, both for milk production and for beef production. One writer has advanced the idea that man could have equal success in improving the elephant by cross-breeding, as in the case of other animals. Elephants, however, do not as a rule breed well in captivity, although a number of successful births in captivity have been recorded. (See page 86.) On the other hand, it requires ordinarily at least 13 to 16 years [2] to bring these animals to sexual maturity, and growth continues for decades thereafter. Consequently breeding for the improvement of the elephant species would necessitate a costly program over many decades. No individual has felt justified in attempting this, not even the fabulously rich princes of India, nor has the English government felt that such a program was worthy of entertainment.

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[1] Noback, C. V., 36th An. Rept., New York Zool. Soc., 1932, p. 58.

[2] Dover, C., Journ. Bombay Nat. Hist. Soc., 1932, **36**, p. 244.

The experience in feeding and breeding animals in zoos and parks has contributed to real knowledge of the maintenance of animals, not only young but adult. It is believed that animals in captivity at the present day in intelligently managed zoological parks are fed both qualitatively and quantitatively as well as they would be when searching for their own food in the wild.

The improved conditions for animal life and growth in modern, scientifically conducted zoological parks are emphasized by the experience at the Hagenbeck Tierpark in Germany, that elephants born in captivity at the park have been found by comparison to be in better condition than elephants born in freedom in India. Dr. Zukowsky of the Carl Hagenbeck Tierpark has given us the privilege of quoting in table 1 a comparison of body measurements on elephants born of newly captured mothers in India with measurements on an elephant born in captivity in Germany. Of these elephants the first six were born in farther India and the next two in India proper. The last, Minjak, was born in Essen in the Hagenbeck circus. The dates of birth of these animals are known exactly. The measurements of the height at the back and at the shoulder (the weights are not given) were made in August 1934, when the elephants from India were received at the Hagenbeck Tierpark. Dr. Zukowsky emphasizes that the large size of the elephant Minjak, born in Germany, is not an accident, for all elephants born in German parks (in Berlin and in Munich) have been of this unusual size. It has been his experience that animals born in parks develop into stronger and larger animals. He and Professor Matschie have shown from a great deal of comparative data obtained at the Berlin museum that the shoulder blades of lions and tigers born and raised in parks are actually longer and wider and likewise stronger than those of free-living animals. The same

TABLE 1—*Heights of elephants born in captivity, subsequently measured at the Hagenbeck Tierpark*

Elephant[1]	Date of birth	Height in Aug. 1934	
		Back	Shoulder
		cm.	*cm.*
Taku	Apr. 1, 1932	156	145
Kathol	Mar. 5, 1932	152	145
Pato	Mar. 1, 1931	148	140
Hungoli	Nov. 3, 1930	130	125
Manjula	Jan. 28, 1930	147	137
Letschimi	Apr. 13, 1930	150	145
Jenny	Feb. 4, 1932	138	132
August	Nov. 15, 1933	95	91
Minjak	Jan. 29, 1932	165	158

[1] The first eight were born in India. Minjak was born in Germany, in captivity.

superiority of growth and breeding of park animals has likewise been observed with lions and zebus (*Bos indicus major*). Zukowsky points out that a gnu bull (*Gorgon albojubatus*) born in Berlin was a hand's breadth higher in the withers than the same kind of adult animals coming from the wild.

SEARCH FOR A SUITABLE ELEPHANT FOR THE GASEOUS METABOLISM STUDY

In outlining the experimental program, emphasis was laid upon the selection of an elephant especially suited for gaseous metabolism measurements, and the research was not begun until an elephant and conditions suitable for this type of observation were available. As the determination of the metabolism necessitated that the animal remain for several hours inside a respiration chamber or that its trunk be confined in a special apparatus for measuring the products of respiration in the air issuing from the trunk, the elephant selected for the gaseous metabolism study had to meet certain requirements. To rule out the factor of growth and avoid the element of extreme old age, an adult animal in the full vigor of middle age was preferred. Inasmuch as a warm-blooded animal of maximum size was desired, obviously the larger the elephant used for the study the better. To minimize the effect of extraneous muscular activity, an elephant with minimum activity, not too restless, and not a "weaver"[1] was essential. Other desired characteristics were that the elephant be as nearly as possible in perfect health, reasonably tractable and non-temperamental, able to adjust itself to new environments, cooperative, and preferably one not associated with a group of elephants but one that could be used alone, not dependent upon its mate or members of a herd for happiness and contentment. Frequently captive elephants work together in a pair or groups and are so disturbed and restless when separated that the main object of the metabolism research, that is, the measurement of the metabolism with the elephant in the greatest degree of repose, would be instantly defeated if this type of animal were employed. Consequently the elephant to be chosen for the study had to be one that was accustomed to working alone. A female rather than a male was desired, as the females are known to have a more tranquil, docile nature. From the standpoint of adaptability to a respiration chamber or trunk-breathing appliance, a circus elephant was preferred to one in a zoological park. Many zoological park elephants are ruled out because of their youth and intractability, and the older elephants in the parks are frequently of extreme age or have proved to be intractable for exhibition purposes in circuses. Furthermore these zoological park elephants are not accustomed to daily handling and transportation, having lived in the same environment for many years, and do not receive much exercise, especially in the winter. The circus elephant, on the other hand, is accustomed to new surroundings nearly every night while on tour, and hence would probably not be disturbed by having to adjust itself to a strange experimental environment. In the proposed gaseous metabolism study there must be close cooperation between the keeper and the animal, on the one hand, and between the keeper and the experimenter, on the other. Therefore, a non-temperamental keeper also was important.

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[1] A characteristic side-to-side movement of the elephant, the weight being shifted from left front leg to right front leg and the reverse.

No stone was left unturned to get in touch with the various elephants available. The first thought was to proceed to Sarasota, Florida, where the Ringling Brothers Circus (Ringling Brothers-Barnum & Bailey, Combined Shows, Inc.) has its winter quarters. But the expense of transporting equipment to Florida and building there a respiration chamber for observations that would occupy perhaps not more than two weeks seemed unjustifiable. When the splendid herd of the Ringling Brothers came to Boston in the spring of 1935 and (through the courtesy of Mr. S. W. Gumpertz, General Manager) were examined by the writer, it was discovered that practically all were weavers and accustomed to being associated with other elephants, and that it would have been difficult to have placed any one of them alone in a respiration chamber. To the ordinary on-looker at a circus or at a circus procession the elephant appears to be indifferent to its environment and not particularly nervous. As a matter of fact, however, the elephant is given to sudden bursts of emotion or excitability, and one can easily imagine what an excited 4000-kg. elephant would do inside a fragilely constructed respiration chamber. One blow of the trunk or the foot would demolish the equipment, or if the elephant decided to walk through the wall of the chamber, nothing would stop it. Sufficient emphasis can hardly be laid upon the inherent excitability of these great beasts. Under ordinary conditions they are tractable and quiet, but if any sudden noise or incident takes place, they may go on a stampede and then are practically uncontrollable; hence a quiet, placid elephant was imperatively needed.

Numerous contacts both in the United States and in Europe were established, to find a suitable animal and suitable conditions for this complicated study of the respiratory metabolism. Among the relatively few promising potentialities one particularly fine elephant at Nashua, New Hampshire, owned by Mr. John T. Benson, the well-known animal man, was offered for use. This animal, although most ideal in every other way, did not have the maximum size desired. Thus, as each individual animal was more closely surveyed, impracticable features were found, sometimes distance, sometimes expense, more frequently the characteristics of the animal itself.

THE ELEPHANT "JAP"

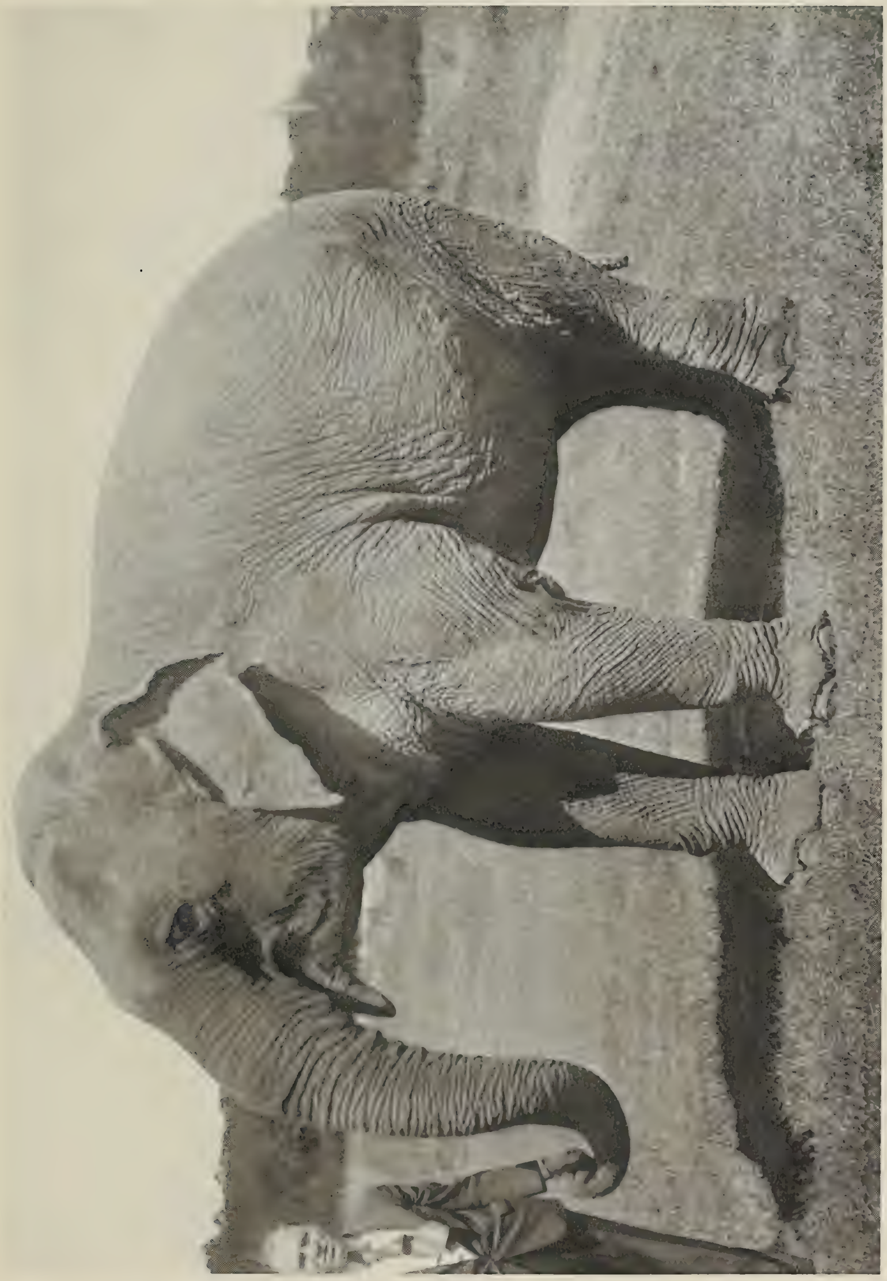
In the fall of 1934 we were informed by Mr. B. M. L. Ernst of New York City that an unusually large elephant had been housed in the basement of the Hippodrome in that city. Through the courtesy of Mr. Ernst and his contacts with theatrical and exhibition people, the owners and the place where this animal was kept were finally, after several weeks' effort, located. This animal was a female Indian elephant named Jap, which had been used almost exclusively for exhibition purposes, having appeared in several theaters of New York and environs in spectacles and plays, practically always alone. The first time we saw her she was temporarily quartered in a small stable in New York City, entirely alone, without any other elephants or other accompanying pets that are so commonly associated with elephants. From this standpoint she was, therefore, an ideal solo animal. On a visit to New York subsequently, this very large elephant was seen on the streets with an advertising banner draped over her, surrounded by children, and in charge of a young colored man. She gave the impression of being unusually large (an impression subsequently confirmed by measurements of her weight and height), in excellent physical condition, and extremely docile, as evidenced by her particular care not to step on the innumerable children about her. In parading about New York she was utterly indifferent to elevated trains, the rush of traffic and the passing of fire apparatus, seemed non-temperamental and thoroughly conditioned to meet new situations.

Preliminary observations on this elephant and conversations with her keeper suggested that she was an ideal animal for the gaseous metabolism investigation. Final arrangements for her use were made through the good offices of Mr. J. Donald Bish and the liberal scientific spirit of the owner, Mr. Tom Gorman. Mr. Bish, head of the Exhibition Tent Company at Campgaw, New Jersey, had constructed in the fall of 1934 a special barn for this animal, and when we arrived he furnished us with every conceivable convenience. It is difficult to express adequately our appreciation of the important rôle played by Mr. Bish's cooperative spirit in this study.

As already pointed out, in addition to the characteristics desired in the elephant, a cooperative, non-temperamental keeper, thoroughly *en rapport* with the animal was also necessary. When we first saw Jap, her keeper had had exclusive care of her for several months. It, therefore, became nothing less than a tragedy when, owing to unforeseen circumstances, there had to be an eleventh hour change in keepers prior to the beginning of active experimenting with Jap. So far as the animal herself is concerned, however, observations on other elephants since the time of the measurements of Jap have confirmed the belief that she was most ideally adapted for this kind of work. She was in splendid physical condition, as was verified by the inspection of Dr. W. Reid Blair and Dr. Charles V. Noback of the New York Zoological Park, who pronounced her an unusually fine appearing animal. Her age was estimated to be not far from forty years. She certainly was not old, and yet her great size and general appearance suggested that she was by no means immature. (See Plate 1.) She was not a weaver, could work alone, and for the most part, in spite of tradition, was not temperamental. The finding of Jap, therefore, in the winter of 1934-35 was the culmination of twenty-five years' search for a suitable experimental elephant. Jap met most of the conditions outlined as prerequisite, and from the standpoint of the animal alone it seemed as if the setting for the investigation was ideal.

Life History of the Elephant Jap

Unusual pains were taken to trace the life history of Jap, primarily to secure all the information possible with reference to any factors that might have contributed to her apparently acquired immunity to cold. (See page 269.) Unfortunately so little of the stories about Jap can be certified as being correct and so much is based upon general impression that there is little direct evidence to explain the immunity to cold noted with her and commented upon in later sections of this monograph. From conversations with many elephant men, consulted separately, it has been possible, how-



Jap, the female Indian elephant used in the gaseous metabolism study.

ever, to piece together a reasonably probable story of her life, which is as follows: Jap was brought from Europe to the United States by Barnum in 1902, at which time she was three or four years old and had a height of about 4 feet (weight unknown). She was with the Barnum show in Bridgeport, Connecticut, for a number of years and then with the Ringling show. From 1920 to 1932 she was with various circus outfits and at times in the hands of V. H. Walker (now director of a zoo in Manchester, New Hampshire). Captain Walker brought her to Jersey City, New Jersey, to the quarters of the Gorman Circus in 1933, since which time she has been with this circus. She was first quartered at Campgaw, New Jersey, in September 1934, and our observations on her began in the spring of 1935.

OTHER ELEPHANTS STUDIED

Although in any physiological study the thesis may be laid down that the findings on any one animal, provided this animal be normal, will in general apply to this species of animal as a whole, nevertheless this is not invariably the rule. For this reason observations were made on other elephants (all Indian) in addition to Jap, including (1) a herd of thirty-four female elephants owned by the Ringling Brothers and Barnum and Bailey Circus, while they were on tour in Boston, subsequently in Bangor, Maine, and later in Sarasota, Florida; (2) two female elephants at the zoological garden at Franklin Park, Boston; (3) one female at the Benson Park in Nashua, New Hampshire; (4) nine elephants (one male and eight females) owned by the Downie Brothers Circus, while on exhibition in Newton, Massachusetts; and (5) the unusually interesting working herd of eighteen female elephants exhibited by the Al. G. Barnes Circus, at St. Stephen, New Brunswick. Through the kindness of Professor Hugh Grant Rowell of Columbia University contacts were established with Captain William Curtis, who extended to us every courtesy and made possible an especially valuable study of this herd of working elephants. Respiration experiments were not made with any of these elephants, but information was secured as to their general habits, respiration rate, heart rate, skin temperature, and particularly the nature and composition of the feces and urine.

Our study of the elephant was thus confined exclusively to the Asiatic species. As is well known, the African elephant differs from the Indian elephant in a number of pronounced anatomical characteristics, and undoubtedly the food of the African is not altogether the same as that of the Indian. There is no reason to believe, however, that because of these differences there would be any great difference in the physiology of these two species of elephant. Until the African elephant is more completely studied, therefore, it can be assumed that what is reported in the following pages for the Indian elephant applies likewise to the African elephant.

PHYSICAL CHARACTERISTICS OF ELEPHANTS STUDIED

The elephants upon which our various observations were made (whether these were body-temperature measurements, urine analyses, respiratory exchange determinations or some other type of measurement) are listed in table 2. For purpose of identification with the particular circus or zoological park to which these elephants belong, the name and owner of

TABLE 2—*Physical characteristics of elephants studied*[1]

Elephant No.	Body weight[2]		Approximate age (years)	Height at shoulder			Name	Owner
	Pounds	Kilograms		Feet and Inches		Meters		
1	8095	3672	40	8	1	2.46	Jap	T. Gorman
2	6820	3090	26	8	2	2.49	Tony	Franklin Park, Boston
3	7310	3320	40	8	1	2.46	Waddy	" " "
4	5640	2560	11	7	5	2.26	Betsy	Benson Animal Farm, Nashua, N. H.
5	3300	1500	11	6	3	1.91	Babe	Downie Bros. Circus
6	3270	1480	10	6	3	1.91	Cora	" " "
7	5065	2300	22	7	8	2.34	Teddy	" " "
8	5535	2510	65	7	2	2.18	Pinto	" " "
9	2310	1050	7	6	0	1.83	Inez	" " "
10	2720	1230	8	5	11	1.80	Marion	" " "
11	4100	1860	16	6	9	2.06	Teenie	" " "
12	4925	2230	65	7	0	2.13	Queen	" " "
13	3210	1460	6	5	8	1.73	Addie	" " "
14	4500	2040	20	7	1	2.16	Mary	Ringling Bros. Barnum & Bailey Show
15	6700	3040	35	7	5	2.26	Nellie	" " " " "
16	4560	2070	20	7	3	2.21	Mabel	" " " " "
17	4530	2060	20	6	11	2.11	Rose	" " " " "
18	5860	2660	40	7	6	2.29	Juno	" " " " "
19	4960	2250	20	7	0	2.13	Jewel	" " " " "
20	4555	2070	20	7	0	2.13	Emma	" " " " "
21	9180	4160	48	7	10	2.39	Big Modoc	" " " " "
22	5820	2640	50	7	6	2.29	Hattie	" " " " "
23	5680	2580	40	7	2	2.18	Little Modoc	" " " " "
24	7810	3540	45	7	8	2.34	Palm	" " " " "
25	4900	2220	20	6	11	2.11	Marcella	" " " " "
26	5360	2430	55	7	4	2.24	Fannie	" " " " "
27	5910	2680	55	7	9	2.36	Jennie	" " " " "
28	6800	3080	35	7	9	2.36	Clara	" " " " "
29	7860	3570	50	8	2	2.49	Liz	" " " " "
30	4500	2040	20	7	1	2.16	Jess	" " " " "
31	4940	2240	20	7	4	2.24	Alice	" " " " "

32	3800	1720	20	6	11	2.11	Bingo	“ “ “ “ “
33	6375	2890	38	8	0	2.44	Bunny	“ “ “ “ “
34	6415	2910	45	7	7	2.31	Katy	“ “ “ “ “
35	6635	3010	42	7	10	2.39	Babe	“ “ “ “ “
36	6875	3120	50	7	6	2.29	Queen	“ “ “ “ “
37	4335	1970	50	6	7	2.01	Dutch	“ “ “ “ “
38	4450	2020	20	7	0	2.13	Eva	“ “ “ “ “
39	7150	3240	45	7	10	2.39	Pinto	“ “ “ “ “
40	4550	2060	35	6	8	2.03	Hazel	“ “ “ “ “
41	4000	1810	20	6	8	2.03	Blanche	“ “ “ “ “
42	5800	2630	60	7	7	2.31	Yasso	“ “ “ “ “
43	8920	4050	55	8	0	2.44	Myrtle	“ “ “ “ “
44	6900	3130	45	7	5	2.26	Tillie	“ “ “ “ “
45	6200	2810	55	7	8	2.34	Wilhelmina	“ “ “ “ “
46	6680	3030	58	7	8	2.34	Topsy	“ “ “ “ “
47	6500	2950	58	7	7	2.31	Trilby	“ “ “ “ “
48	6200	2810	35	7	2	2.18	Ruth	Al G. Barnes Circus[3]
49	6300	2860	30	7	5	2.26	Tony	“ “ “ “
50	8000	3630	30	8	0	2.44	Floto Jenny[4]	“ “ “ “
51	8252	3740	36	8	3	2.52	Jewel	“ “ “ “
52	9098	4130	37	8	3	2.51	Babe	“ “ “ “
53	9000	4080	38	8	4	2.54	Trilbie	“ “ “ “
54	3000	1360	15	7	3	2.21	Dollie	“ “ “ “
55	3200	1450	15	7	3	2.21	Minnie	“ “ “ “
56	8000	3630	40	7	7	2.31	Barnes-Show Jenny[4]	“ “ “ “
57	9053	4110	26	8	0	2.44	Freida	“ “ “ “
58	3150	1430	16	7	3	2.21	Mary	“ “ “ “
59	5354	2430	20	7	6	2.29	Palms	“ “ “ “
60	8198	3720	35	8	0	2.44	Pearl	“ “ “ “
61	5300	2400	20	7	6	2.29	Lois	“ “ “ “
62	7000	3180	26	7	11	2.41	Kass	“ “ “ “
63	7200	3270	25	8	3	2.51	Josky	“ “ “ “

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[1] All the elephants were females except No. 7. All were Indian elephants.

[2] The weights of elephants Nos. 4 to 13 and Nos. 48 to 63 represent approximate, estimated weights. The weights of the other elephants were accurately determined on scales. In the case of the Ringling herd, one-third of the weights were furnished recently through the kindness of Edward Doherty and two-thirds through the kindness of Larry Davis.

[3] There were actually 18 elephants in the Barnes herd. These were available for a general study of their habits, but two of them were not subjected to any special, individual measurements and hence are not listed in this table. The Barnes circus formerly also owned a male Indian elephant, Vance, weighing 9054 pounds or 4110 kg.

[4] “Floto Jenny” was obtained from the Floto Circus. “Barnes-Show Jenny” had been a member of the Barnes herd for a long time.

each animal have been given, together with the actually measured or estimated weight, age, and height of each, so far as the data are available. For purpose of ready reference in the discussion of results which follows on pages 61 *et seq.*, a number has been assigned to each elephant. Throughout the text the elephants other than Jap will usually be mentioned by number rather than by name; as a rule the particular identity of each individual elephant will have no significance and, if needed, can be found by reference to table 2. As a matter of convenience, Jap has been assigned the number 1, and the Barnes herd, which is characterized as being typical of a herd of working elephants, have been given the last numbers in the list, *i. e.*, from 48 to 63.

CHRONOLOGY OF THE RESEARCH

When contact was finally made with the elephant Jap, an agreement with the owner permitting her use in the metabolism measurements was concluded on February 13, 1935. The research progressed rapidly thereafter, as the following chronological history will testify:

1935	
Feb. 12, 25	Trips to Campgaw, New Jersey, for inspection of local conditions.
Feb. 15	Construction of respiration chamber authorized.
Feb. 20 to Mar. 6	Collection and testing of accessory apparatus in Boston and express shipments to Campgaw.
Mar. 6	Construction of respiration chamber at Campgaw completed.
Mar. 6	Transportation of equipment and personnel from Boston to Campgaw.
Mar. 7 and 8	Apparatus unpacked, assembled, and tested for tightness and accuracy of functioning.
Mar. 9	Jap inside respiration chamber for first time.
Mar. 17	First series of experiments ended.
Mar. 21	Apparatus shipped to Boston.
Mar. 22 to 24	Respiration chamber dismantled.
Apr. 2 to 12	Second series of measurements on Jap at Campgaw, for study of digestibility and urine and feces temperatures.
May 9 and 11	Observations in Boston on the thirty-four elephants of the Ringling herd.
June 18 July 23 Sept. 25 Nov. 6	Observations on two elephants at Franklin Park, Boston.
July 1	Second series of observations on the thirty-four elephants of the Ringling herd, in Bangor, Maine.
July 16	Observations on nine elephants of the Downie Brothers, in Newton, Massachusetts.
Aug. 1	Observations on eighteen elephants of the Al. G. Barnes Circus, in St. Stephen, New Brunswick.
Sept. 27 and Oct. 7	Observations on elephant at Benson's Animal Farm, Nashua, New Hampshire.
Nov. 12	Heart rate study on Jap at Campgaw, New Jersey.
Nov. 15 to 21	Third series of observations on the thirty-four elephants of the Ringling herd at Sarasota, Florida.

TECHNIQUES EMPLOYED

To accomplish the various measurements listed in our plan of research (see pages 13 to 15), a considerable amount of well-known apparatus and some newly constructed and hitherto undeveloped apparatus (particularly for the gaseous metabolism measurements) were necessary. The equipment other than the respiration apparatus was as follows.

TECHNIQUES OTHER THAN THE RESPIRATION CHAMBER

Weights—For the weight of the elephant Jap the certified municipal scales of Campgaw, New Jersey, were used. For the weights of feed, feces, and urine, "silk scales" (Plate 6, page 56), capable of weighing to 150 kg. with an accuracy of 10 grams, were employed.

Temperature measurements—The thermometers for measurements of environmental temperature and temperatures of urine, feces, and drinking water were calibrated, standard Centigrade thermometers, graduated in tenths and readable to hundredths of a degree, and calibrated, self-registering (Fahrenheit) clinical thermometers. One recording thermometer was also used in the barn, on the outside wall of the respiration chamber (shown in the upper right-hand corner of Plate 6, page 56). The technique of the measurement of skin temperature has already been adequately described.[1] Briefly, the apparatus consists of two copper-constantan thermo-junctions, a thermostat, and a galvanometer. One of the junctions is placed in water in a thermos vacuum bottle with electrically controlled thermostat to hold the temperature of the water at any desired level. In the study with the elephant this was not far from 30° C. The junction placed on the skin is shaped like a wire hairpin and has a backing of cotton batting in hard rubber. The lead between the galvanometer and the junctions was, in this case, about two or three meters long so that the operator could reach about the elephant fairly easily and apply the junction at various points.

The temperature of the expired air, which has heretofore not been measured with animals, was measured in the case of the elephant by noting the temperature of the exhaled air as it left the proboscis. For this purpose an apparatus was employed, the details of which have not yet been published. This apparatus as used with humans was described at the November meeting of the National Academy of Sciences in Cleveland, Ohio, in 1934.[2] Its principle is essentially that of the skin-temperature apparatus save that extremely fine junction wires are used and a rapidly acting galvanometer is necessary. Ideally an extremely sensitive, precise galvanometer is desirable for such measurements, either the string galvanometer or the more practical Moll galvanometer. To facilitate the transportation of the apparatus with its delicate thermo-junction wires, however, a portable

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[1] Benedict, F. G., Proc. Nat. Acad. Sci., 1925, **11**, p. 549; Benedict, F. G., V. Coropatchinsky and M. D. Finn, Journ. de Physiol. et de Pathol. gén., 1928, **26**, p. 1; *idem,* Leopoldina (Amerikaband), Berichte d. kaiserl. Leopoldinischen Deutsch. Akad. d. Naturforscher zu Halle, 1929, **4**, p. 129.

[2] Benedict, F. G., and C. G. Benedict, Science, 1934, **80**, p. 546.

Leeds and Northrup galvanometer was employed in studying the temperature of the expired air of Jap. Fortunately since the expiratory blasts of the elephant were of such relatively long duration, it is believed that the records on this galvanometer were reasonably correct. The indications were that the maximum excursion of the galvanometer had taken place in each measurement. In all probability the true temperatures of the expired air of Jap were a few tenths of a degree higher than those recorded by this apparatus. In subsequent experiments with some of the other elephants, a Moll galvanometer was found more satisfactory and could be used in conjunction with the technique for getting the heart rate.

Heart-rate technique—The only satisfactory measurements of the heart rate of the elephant are those made by Alexander Forbes,[1] who employed the string galvanometer. Since this was impractical to transport, use was made of part of the Boas cardiotachometer,[2] that is, the radio amplification system. Actual tests showed that the relay and counter used by Boas could not well be used for the elephant; therefore, two material alterations were made, in that the relay and counter were replaced by the Moll galvanometer with telescope and scale, and a series of condensers (from two to six micro-farads) were used to cut out the effects of the at times very considerable extraneous muscular movements.

Chemical analyses of samples of the hay and feces of Jap were made through the kindness of Professor E. G. Ritzman at the University of New Hampshire by use of the well-known standard methods of the Association of Official Agricultural Chemists,[3] and determinations of the heats of combustion of these same samples were also made at the University of New Hampshire by use of the Parr adiabatic calorimeter. Microscopic examinations of samples of urine and feces were made by the usual clinical methods, the benzidine test was applied to samples of feces, and determinations were made of the specific gravity of several urine samples, in the laboratory of Dr. Elliott P. Joslin at the New England Deaconess Hospital in Boston, Massachusetts, and in the laboratory of Dr. H. E. Thompson of the Eastern Maine General Hospital at Bangor, Maine. We are indebted to Dr. Joslin and Dr. Thompson for these data and also to Miss H. W. Hunt, Dr. Alexander Marble, and Dr. Howard F. Root of the New England Deaconess Hospital. At the Nutrition Laboratory, thanks to the kindness of Dr. T. M. Carpenter and with the assistance of Miss E. MacLachlan and Miss A. J. Murphy, other chemical analyses of the urine were made. The nitrogen in urine was determined by the Kjeldahl method. The specific gravity of the urine was determined by the urinometer standardized against the Ostwald picnometer and also by the urinometer and the Westphal balance. The allantoin in urine was determined by the method of Larson.[4] All the other urine analyses were made according to the well-known methods of Folin.[1] The drinking water of the elephant Jap at Campgaw was analyzed by the standard methods for water analysis.[2] These painstaking determinations were made by Mr. Amos E. Light of the Department of Chemistry, Columbia University, New York City. For his gratuitous efforts in this work we are grateful.

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[1] Forbes, A., Cobb, S., and McK. Cattell, Amer. Journ. Physiol., 1921, **55**, p. 385.

[2] Boas, E. P., Arch. Intern. Med., 1928, **41**, p. 403; Boas, E. P., and E. F. Goldschmidt, *The heart rate*, Baltimore, 1932.

[3] Official and tentative methods of analysis, Assoc. Official Agric. Chemists, Washington, D. C., 1930, 3d ed., pp. 277-281.

[4] Larson, H. W., Journ. Biol. Chem., 1931-32, **94**, p. 727.

APPARATUS FOR STUDYING THE RESPIRATORY EXCHANGE

The dominant thought in this study was, from the first, the measurement of the elephant's metabolism—under basal conditions, if possible, or if necessary, while the animal was on feed. For such measurements two methods are possible: (1) The attachment of some sort of breathing appliance to the elephant's trunk, with valves for separation of inspired and expired air, a spirometer, and ventilating equipment; and (2) a respiration chamber of suitable size with provision for proper ventilation and for measuring the products of respiration. Of these two methods, obviously the first is the simpler. For the construction of a respiration chamber large enough to hold one of these gigantic animals the cost alone seemed prohibitive, whereas the cost of constructing a trunk-breathing appliance would be relatively small. Because of the uncertainty of the physiological soundness of measuring the total metabolism by an appliance for collecting the expired air from the trunk alone, excluding the mouth, it was necessary to provide for both methods of measurement. In the Nutrition Laboratory's experience in studying the metabolism of man and different animals (the carbon-dioxide production of which has ranged from about 30 milligrams per hour in the case of cold-blooded animals at a low environmental temperature to 250 grams per hour in the case of large domestic animals) the closed-circuit or the open-circuit principle has been used according to the particular condition to be met. A closed-circuit chamber was out of the question with the elephant, as well as a closed-circuit breathing appliance. The largest closed-circuit respiration chamber that has ever been employed was the extremely ingenious construction for the horse by Zuntz,[3] shortly before his untimely death. The technical difficulties in the use of this large system have practically precluded its subsequent use. As a result of the Nutrition Laboratory's experience with the open-circuit principle, first with the so-called "group chamber" for humans in Boston and subsequently with the chamber for large domestic animals at the University of New Hampshire, this principle was the only one seriously considered in the elephant problem. An open-circuit respiration chamber was, therefore, constructed, with suitable ventilating, metering, and aliquoting systems. Since to make suitable analysis of the air from an open-circuit respiration chamber or open-circuit breathing appliance an exact gas-analysis apparatus is necessary, the technique for measurement of the elephant's gaseous metabolism also included use of the Carpenter gas-analysis apparatus. (See page 49.) Supplementing the study of the respiratory exchange, measurements of the total water-vapor output were made by the use of a new form of chemical hygrometer devised by Carpenter. (See page 50.) Consideration will be given first to the respiration chamber. This will be described in detail, as it was developed especially for the elephant research, has proved satisfactorily accurate, and has supplemented so well the earlier chambers employed for large ruminants and for groups of animals as well as humans.

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[1] Folin, O., *Laboratory manual of biological chemistry,* New York, 5th ed., 1934.

[2] Standard methods for the examination of water and sewage, American Public Health Association, 450 Seventh Avenue, New York, 1933, 7th ed., pp. 26 and 42.

[3] Zuntz, N., Landw. Jahrb., 1909, **38** (Ergänz. Bd. V), p. 473.

Assemblage of apparatus—The planning of the respiratory exchange measurements had to be left until it was known what elephant could be used, who the keeper would be, and where the measurements would have to be made. No general plan could be made that would be adaptable to all elephants under all conditions. But once the animal and the place of experimentation had been decided upon and the size of the barn and the environmental conditions were known, the experimental plan was perfected rapidly in Boston and the respiration chamber was designed and constructed to fit the conditions. Obviously no respiration experiments could be made at the elephant barn in Campgaw, New Jersey, until a chamber was constructed. But during the construction of the chamber the accessory equipment, such as the ventilating apparatus and the meter, could be collected and tested. This was the immediate task as soon as the decision was made to study Jap at Campgaw, and the plans were so made that these various accessories were adjusted to the finally constructed chamber at Campgaw with a precision comparable perhaps only to the precision exhibited by circuses in moving their entire outfits from place to place, frequently on consecutive nights, disassembling the outfits at night and reassembling them the next morning.

Transportation of apparatus—Inasmuch as it was impossible to study Jap at the Nutrition Laboratory, the development of the highly specialized techniques and particularly their adaptability to the special problems in hand necessitated that consideration be given not only to the accuracy of functioning of the various pieces of apparatus but also to the safety of the transportation of the apparatus from Boston to Campgaw, New Jersey, the reassembling there, and the adjustment to the quarters where the investigation was to be carried out. This latter consideration entered into the construction of every piece of apparatus. Certain parts, such as the spirometers, ventilating apparatus, gas meters, and sampling pumps, could be readily transported and were sent by express. Other parts, such as the delicate glass gas-analysis apparatus of Carpenter and the chemical hygrometer could not be shipped intact by express with insurance of safe arrival. Hence transportation of these parts was undertaken by automobile. Consequently the study of the gaseous metabolism took on much of the nature of field work, as the distance from the Nutrition Laboratory in Boston to Campgaw, New Jersey (about 250 miles or over 400 kilometers), called for a nearly complete collection of replacement parts to make repairs in the field, if necessary. It is a tribute to the skillful packing of the gas-analysis apparatus by Dr. T. M. Carpenter and to the care in packing of other instruments by Mr. Robert C. Lee and his solicitous care en route that the entire equipment was transported without breakage and was unpacked and ready for use a few hours after arrival at Campgaw.

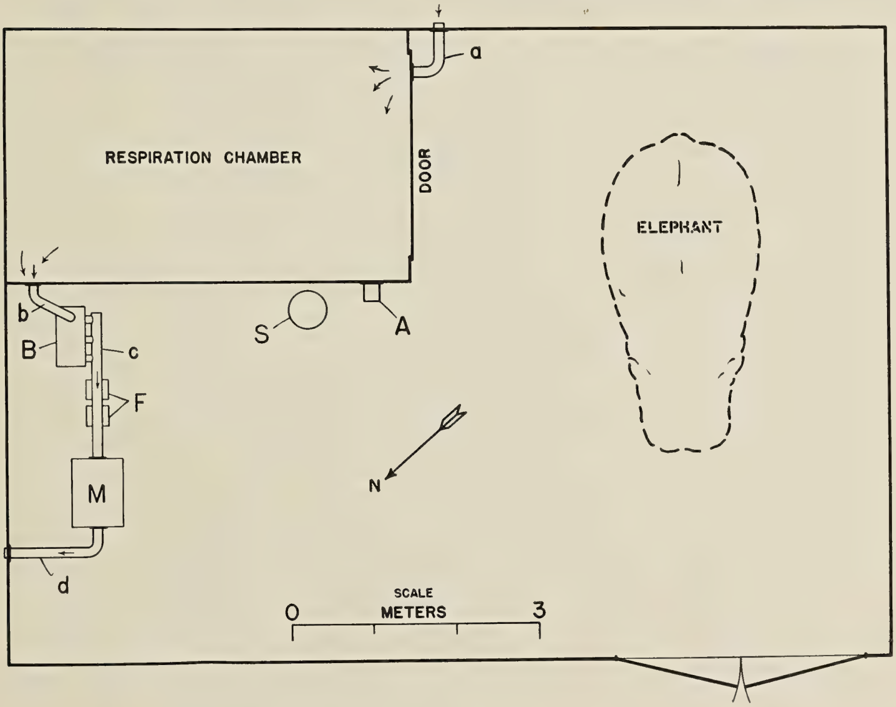
Barn arrangements at Campgaw—Almost the first step taken prior to the construction of apparatus in Boston was to make a survey of the local conditions at Campgaw, particularly of the elephant barn and nearby buildings. This determined in large measure the type of construction and location of the respiration chamber and the disposition of the ventilating and metering apparatus. The barn where Jap was housed was simply constructed of single-thickness boards, nailed to studs to form the sides of the building, and had no floor. It was about 11 meters long, 8 meters deep, and 4 meters in height from the floor to the eaves or lowest part of the sloping roof. Thus it was large enough to permit the installation of the respiration chamber and accessory parts and at the same time the proper chaining of the elephant when she was not in the chamber. Owing to the earliness of the season, it was inadvisable to place the chamber outdoors, although Jap was inured to the cold. The east corner of the barn was, therefore, used for the chamber, and the elephant, when not having its metabolism measured, was at one end of the barn near the doors. Electric current was available, and there was a stove for local heating in the north corner of the barn. This stove did not suffice to keep the temperature anywhere near as high as ordinarily prevails in an elephant house in a zoological park, *i. e.*, 20° C. In Plate 2A one sees the elephant in place in the barn, with the barn doors partly open and the westerly corner of the respiration chamber in the rear at the left faintly indicated.

Floor plan of the barn and general arrangement of respiration apparatus—The floor plan of the barn showing the approximate location of the chamber and other apparatus is illustrated in Plate 2B. As the chamber was constructed in a corner of the barn, the two walls of the building formed a support or framework, but not sides, for two sides of the chamber, and for the rest of the framework it was necessary to construct only the floor, the top, one side, and the entrance end of the chamber. The position of the elephant when not in the chamber is indicated by the outline (broken line) of her body in the southwest end of the barn. Since Jap was of such huge size and could stretch a distance, even though confined with short lengths of chain, it became a problem to give her suitable space for confinement and at the same time distribute the movable parts of the respiration apparatus so as to keep them out of her reach. From where she was chained on the floor of the barn she could reach with her trunk as far as the tube A on the side of the respiration chamber. All movable parts of the apparatus were, therefore, placed at the northeast end of the barn beyond the reach of her trunk. The animal was in no sense vicious but naturally curious, and inasmuch as she spent many hours at night practically unwatched, although not unattended, no apparatus that might be destroyed could be left within her reach. The door of the respiration chamber, at the southwest end, was provided with a pipe, a, for the introduction of outdoor air into the chamber. The opening A was covered with a cap of rubber dam and served as a speaking tube in the respiration experiments and as a support for the trunk-breathing appliance in the experiments made with the elephant's trunk inside a breathing appliance. (See page 56.) Air left the chamber at the upper north corner, through the pipe b, descended into the blower box B, containing three vacuum cleaner blowers, then through the pipe c leading into the meter M, from which it was discharged through the pipe d outdoors. The two boxes marked F represent the device for collecting aliquot samples of the outcoming chamber air for subsequent gas analysis. They will be described later. (See page 44.) In those experiments in which the respiratory exchange from the trunk of the elephant alone was measured, a large 100-liter spirometer was placed in the location marked S. The connections from this spirometer to the blower box B are not shown in Plate 2B, but are shown in figure 5 (p. 59).

THE RESPIRATION CHAMBER PROPER

Size of chamber—Since the elephant is not only very large but, from its anatomical shape, able to reach extensively in all directions and thus do damage, one suggestion was to build a chamber of such size that Jap could not reach the walls or top with her trunk, even when standing on her hind legs (although in this latter case the fore legs could be chained down). There is an optimum size for a respiration chamber which can not be deviated from too widely. Much erroneous experimental material has been published, based upon the use of a chamber altogether too large for the particular animal studied, with consequently great inherent errors in the measurements. In general a respiration chamber containing a minimum amount of extraneous air and at the same time not unduly restricting the animal is the ideal. Minimizing of the volume of extraneous air reduces the correction in the measurements necessitated by the change in composition of the residual air between the beginning and end of the experiment. To study a 20-gram mouse in an 8-liter chamber or a 40-kg. boy in one of 100 cubic meters is debatable technique. In the design of a respiration chamber it is necessary to have an approximate idea as to the probable metabolic activity of the animal, for the size of the chamber, the rate of ventilation of the chamber, and the metering device for measuring the volume of outcoming chamber air will depend upon the metabolic rate. Our first estimate was that the elephant would probably produce about 15 liters of carbon dioxide per minute, and the construction of the respiration apparatus was based upon this estimate, with a rather wide limit. The size of chamber finally decided upon was 4.73 meters long, 3 meters wide, and 3 meters high (inside dimensions). This was a comfortable size not only for the elephant but for the people handling her and included space for the keeper to stay inside with the animal. When the chamber was designed, it was hoped to be able to induce the elephant to lie down in it so that the metabolism could be measured in the lying as well as in the standing position. Subsequently it was found that this could not be done, because the trainer could not persuade the animal to lie down. It further developed that the chamber (although through no fault of the engineer who constructed it) was too narrow to make it wise for the elephant

A—Elephant Jap inside the barn, and respiration chambers in the rear.



B—Floor plan of elephant barn.

a, pipe for introduction of outdoor air into respiration chamber; b, pipe for outcoming chamber air; B, blower box; c, pipe connecting blower box with aliquoting system, F, and meter M; d, pipe through which air leaving meter was discharged outdoors; A, short length of pipe covered with rubber dam, which served as a speaking tube in respiration chamber experiments and as a support, in other experiments, for the trunk-breathing appliance; S, spirometer used in trunk-breathing experiments. Dotted outline of elephant indicates position of animal when not inside the chamber.

to lie down. Jap herself is 8 feet 1 inch (2.5 meters) high and as the chamber was only 3 meters high and 3 meters wide, it would have been almost impossible to have centered her position in the chamber so that when she made the last movement in lying down she would not have come in contact very heavily with the thin metal walls and possibly have damaged them. The likelihood of a chamber of this size being again constructed is slight. But in case such construction is ever contemplated by any one, it is recommended that the chamber be made somewhat wider, if there is any thought of having the elephant lie down inside the chamber.

Volume of Chamber—The total volume of the chamber, not corrected for the volume of the elephant, was 43,000 liters. Since the elephant weighed about 4000 kg., one can assume that its volume was not far from 4000 liters or about 9 per cent of the total volume of the chamber. The respiration chamber for large ruminants at Durham, New Hampshire, has a total volume of 9640 liters. A steer weighing 600 kg. and having a volume of about 600 liters would, therefore, displace only about 6 per cent of the total volume of the chamber. Thus the elephant chamber had a relatively smaller volume of extraneous air than the Durham chamber. Similarly, the clinical respiration chamber for humans[1] used at the Nutrition Laboratory has a volume of 550 liters, and a subject weighing 60 kg. would displace about 11 per cent of this volume. In spite of the apparently huge size of the elephant chamber, the volume of extraneous air around the animal was not disproportionately greater than is the case with other commonly used respiration chambers. Obviously the larger the volume of residual air, the larger the volume of carbon dioxide residual in the chamber and the greater the correction to be made for the changes in composition of the residual air. But in the case of the elephant, the actual total production of carbon dioxide per half hour was so great that even seemingly large changes in residual carbon dioxide represented relatively no greater correction, percentagewise, in the metabolism measurements than is the case in the respiration chambers for steers and for man. Subsequently it was found that the carbon-dioxide production of the elephant was extraordinarily regular from period to period, so that, on the whole, the correction for change in residual carbon dioxide was insignificant.

Construction of chamber—It was at first considered necessary to have the chamber of such strength that it could not easily be damaged by the elephant's pounding it with the trunk, kicking it with the legs, or pushing against it with the head. But when it became apparent that it would be feasible to have the keeper inside the chamber with the animal, to control it during the experiment and insure absence of any damage by the elephant due to willful destruction, apprehension, or fright, a light-walled, semi-rigid chamber was constructed with no thought of resistance to onslaughts of the animal. The chamber was a shell into which Jap could go of her own accord, and the opening through which she passed could be closed and made air-tight. At no time during the entire series of tests did Jap do any damage to this chamber. Another point in the design of the chamber was to construct it so that by withdrawing air from it at a given rate one could be sure this withdrawn air would be replaced automatically by uncontaminated air. Hence the chamber had to be made sufficiently air-tight so that by means of the ventilating system a slight vacuum could always be maintained. The inexpensive, simple, but effective type of construction employed in the elephant chamber is strongly to be recommended. A construction of similar nature for domestic animals, such as cows, steers, and horses, is conceivable at little expense. This chamber was constructed and in part designed by the engineer, A. H. Ackerman, formerly of the New York Board of Engineers and now of Campgaw, New Jersey. We are greatly indebted to him for his personal interest, ingenuity, and painstaking care, which made the chamber itself a success, especially from the standpoint of tightness.[1]

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[1] Benedict, F. G., and E. H. Tompkins, Boston Med. and Surg. Journ., 1916, 174, pp. 857, 898, and 939.

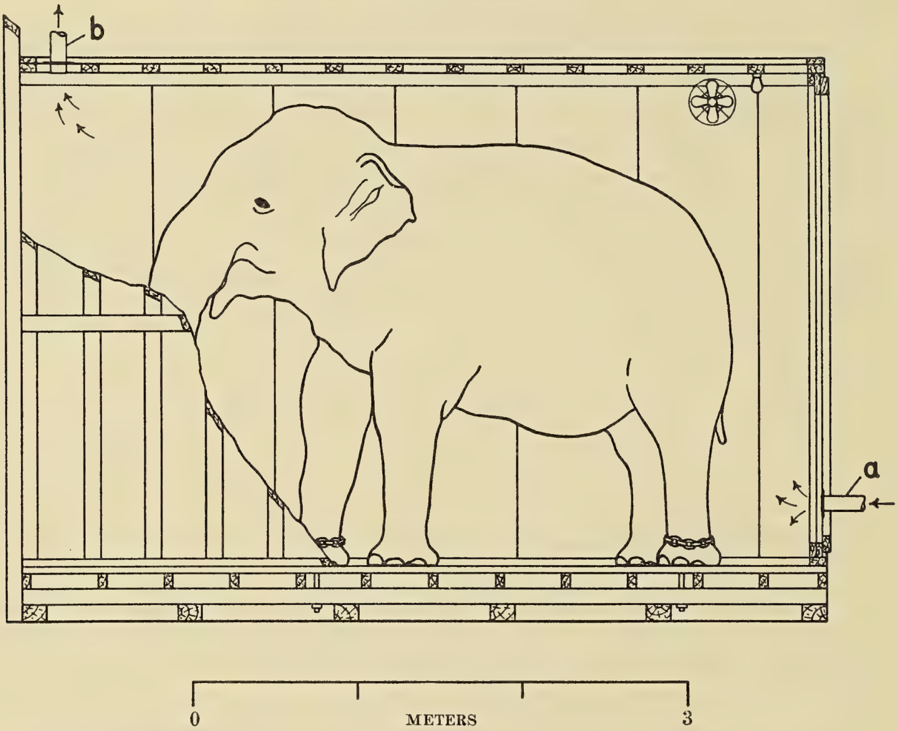

Fig. 1—Side-view drawing of respiration chamber, showing its construction and elephant in place.

a, pipe for introduction of outdoor air; b, pipe for outcoming chamber air.

A side-view drawing of the chamber, with the wall somewhat broken away, showing the construction and the elephant in place, is given in figure 1. The walls of the barn were made of 2- by 4-inch studs (the standard size of lumber much used in building construction), spaced 14 inches on centers. To these, boards were nailed. The walls were made of this strength to withstand any inadvertent movements of the elephant against them. (During our stay at Campgaw Jap did knock off three or four boards from the outside of the barn one night, but never damaged the respiration chamber.) This wall construction furnished the wooden framework for one side and one end of the respiration chamber. The other side, that is, the northwest side of the chamber, was constructed of 2- by 4-inch studs reenforced by a 2- by 4-inch (5 by 10 cm.) brace running horizontally about half-way up the side. The support for the floor was made of six 4- by 6-inch joists laid flat, 36 inches on center, on top of which were laid in the opposite direction three 4- by 6-inch joists 18 inches on center, with a 2- by 4-inch joist on each end. On top of the second set of joists was laid a third set of 2- by 4-inch joists laid in the same direction as the first set. On this support a 1¼-inch fir flooring was finally laid. (For these details see, also, Plate 4, page 34.) The floor was thus solid and substantial enough to support the elephant. The wooden framework for the roof was made of 2- by 4-inch joists placed 14 inches apart, as were the studs on the northwest side.

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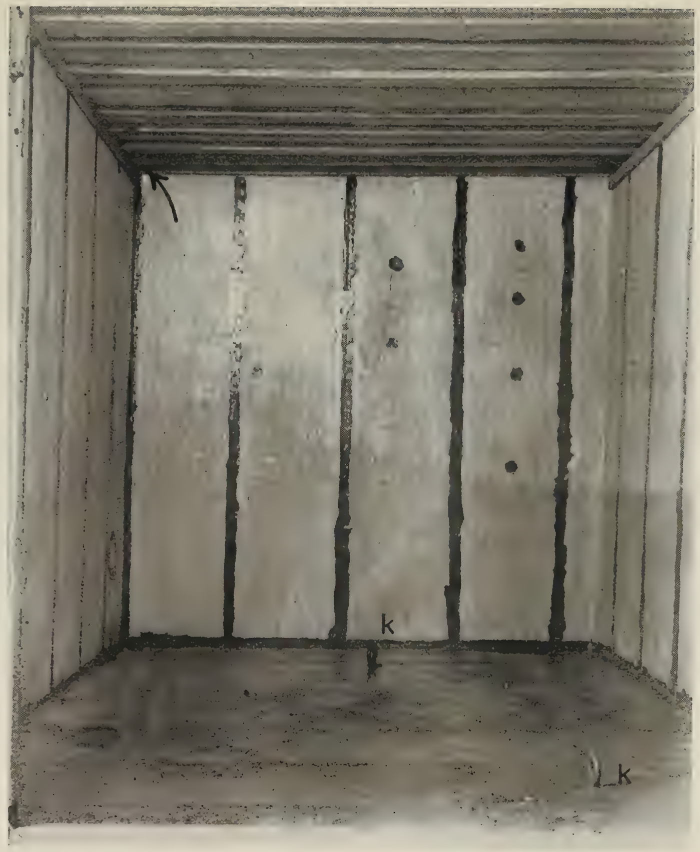
[1] In subsequent information concerning Jap, Mr. Ackerman has given unstintingly of his time and supervision.

Inside the wooden skeleton of the chamber, on the four sides, were placed sheets of galvanized iron (flat steel sheathing), with the edges lapped over each other about one inch (2.5 cm.). Each edge was nailed with a row of nails to the 2- by 4-inch studs forming the side framework. Asphalt roofing cement was first painted on the wood and was then applied under each metal lap, on the outside of the lapped edges, and on the nail heads. The cement was later inspected to make sure none of it had pulled away. Sheet metal was overlapped, nailed, and cemented in this same way on the roof, but instead of the metal being placed on the underside of the wooden skeleton from which it would have to hang, the metal was placed on top of the roof framework, thus adding to the strength of the construction. At the bottom of the chamber sheets of galvanized iron were laid on top of the matched flooring. To aid in the collection of urine, in case any were voided during an experiment, the lapped edges of the metal floor were soldered rather than being nailed and cemented, and the floor was pitched slightly toward the farther or north corner. Here a pipe was soldered into the floor, connecting with a trap outside to collect the urine drained off. No urine was passed during the experiments except on one occasion (March 15, period 4) when a small amount was passed, so this precaution proved unnecessary. The pipe was, therefore, closed with a rubber stopper. The sheet metal floor was continued up the sides of the chamber for a few centimeters. The metal walls were brought down flush to the floor over this turned-up edge and the joint was closed with cement. Thus an essentially air-tight chamber was lightly constructed of inexpensive materials and with incredible rapidity.

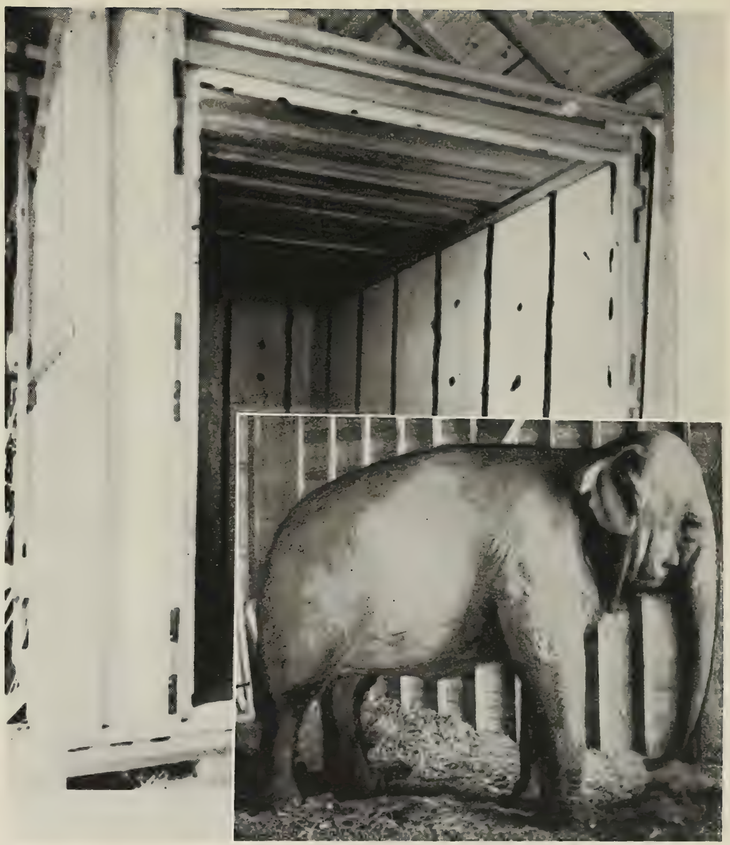
In Plate 3A can be seen the details of the interior wooden support of the roof with the 2- by 4-inch joists laid flat and the absence of wood in any other part of the inside of the chamber. This photograph was taken through the open door of the chamber. The black vertical bands represent the asphalt roofing cement painted over the lapped edges of the sheet metal. The arrow points to the corner where air was withdrawn from the chamber. The structure of the chamber, its location with relation to the corner of the barn, and the black bands on the interior denoting where the seams of the metal were cemented together are shown in Plate 3B. The several black spots indicate where large-headed nails were driven through to hold the sheet metal. These nails were likewise covered with suitable amounts of black asphalt paint. This photograph was taken by the "press" at the time the respiration experiments were being made. The insert is a view of Jap chained to posts driven into the earth of the barn floor. The inside structure of the barn is clearly shown back of her. On the left-hand side of Plate 3B appears rather indistinctly the outside, northwest wall of the chamber, made of 2- by 4-inch studs, with a horizontal 2- by 4-inch brace half-way up. Near the bottom of this outside wall is indistinctly seen the tube (see A, Plate 2B) used for the speaking tube and, in certain experiments (page 56), for support of the trunk-breathing appliance. The details of the outside construction of this northwest wall are somewhat better shown by Plate 4, in which can be seen two of the 2- by 4-inch studs laid flat, with the strip metal nailed on the inside and cemented.

Door closure—The entrance door is likewise shown in Plate 4. This door was made of two large sheets of three-ply wood, a composite wood material, reenforced by a 2- by 4-inch frame around the edge, with two diagonals and one vertical upright through the middle. The interior surface of the door was heavily painted. The one and only seam (vertical) of the door was heavily painted with black asphalt cement, as a final insurance against leakage. A small cleat on the inside, about 2 inches (5 cm.) from the base of the door and running horizontally, made it possible to rest the door on the doorsill and then push the upper part into place, where it fitted neatly. Near the bottom of the door at either side was a metallic handle to assist in handling the door, and at the lower right-hand side was a hole through which was led the pipe, a (10 cm. internal diameter), for the introduction of outdoor air into the chamber. The window, W, was made of a small piece of glass, 20 by 25 cm. in dimensions, attached to the three-ply wood with adhesive tape. The large straps of heavy iron, three on each side of the door, were not used. The first thought was to place bars through these straps to wedge the door in place. This method was cumbersome, took considerable time, and in case of emergency the door could not be removed quickly. A simpler method was, therefore, employed, using the brace pieces m and m, which could be instantly adjusted and instantly removed. The door, as put in place and thus braced, was reasonably tight. In closing doors and openings of respiration chambers of various sizes, it has been the custom of the Nutrition Laboratory to make the closure complete by the use of physicist's wax, a mixture of Venice turpentine and beeswax. This procedure suffices for chambers of moderate size and particularly if the laboratory temperature is approximately 20° C. But the temperature of the barn at Campgaw was usually much below 15° C. The wax was, therefore, very hard and a wax closure for this enormous opening

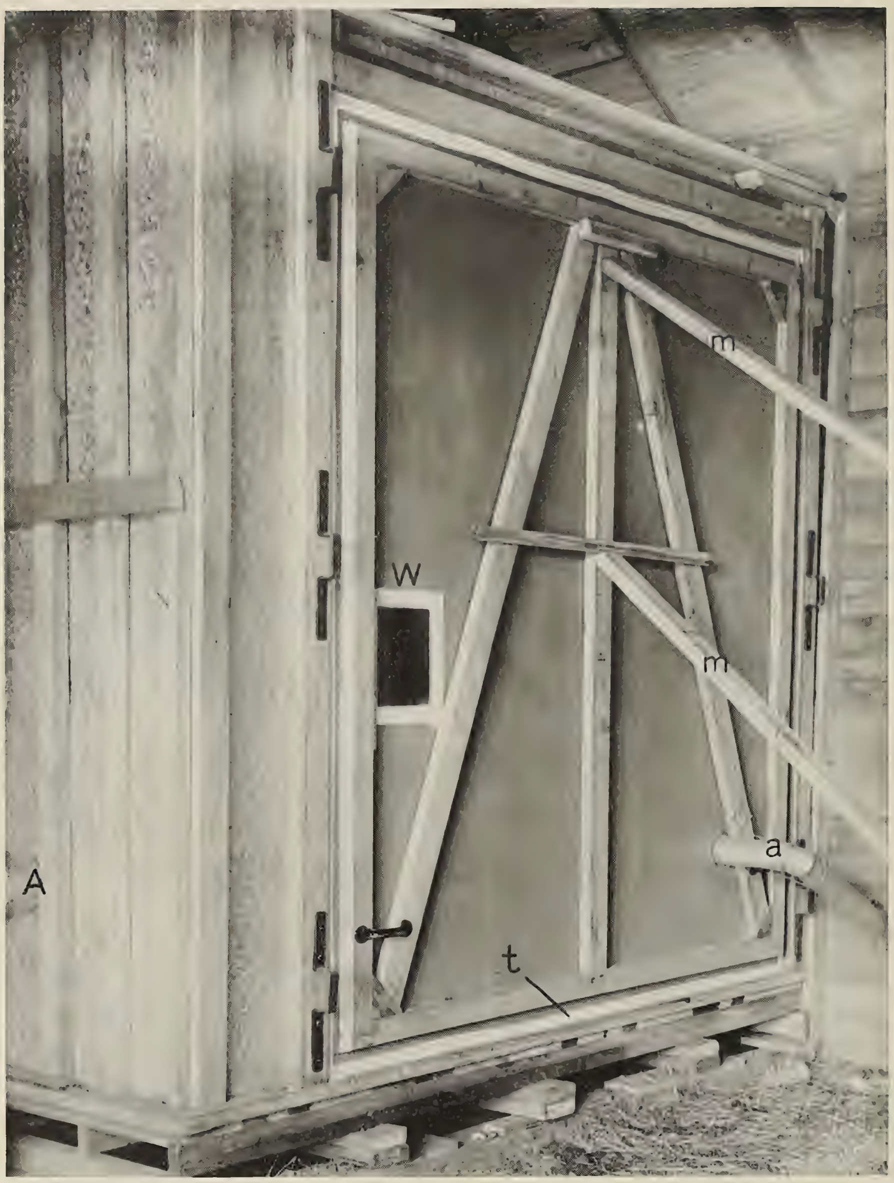


A—INTERIOR OF RESPIRATION CHAMBER, SHOWING WOODEN SUPPORT FOR METAL ROOF AND INTERIOR METAL SIDES, WITH CEMENT PAINTED OVER THE LAPPED EDGES AND NAIL HOLES.

One rear and one front leg of the elephant were chained to the eye-bolts, k, k. The arrow indicates the place where air was withdrawn from the chamber.



B—PHOTOGRAPH SHOWING GENERAL CONSTRUCTION OF RESPIRATION CHAMBER AND ITS LOCATION IN CORNER OF BARN, WITH INSERT SHOWING VIEW OF ELEPHANT JAP.



DOOR CLOSURE.

a, pipe for introduction of outdoor air; W, window; m, m, wooden braces to hold door tightly in place; t, adhesive tape; A, short length of pipe that served as speaking tube or for support of trunk-breathing appliance.

was out of the question. At the suggestion of Mr. Robert C. Lee of the Nutrition Laboratory staff, the closure was made by placing lengths of adhesive tape (5 cm. wide) entirely around the door (see t, Plate 4). The construction of the doorframe was such that the sheet metal came clear around the door jamb. Thus when the door was in place and the tape applied, half of the tape adhered to the three-ply wood of the door and the other half to the sheet metal itself. This made the closure air-tight, and yet by taking hold of the ends of the tapes one could remove them instantly and free the whole door with great rapidity. About five minutes were required to apply the adhesive tape, and less than half a minute was needed to remove it. Because of the inherent irritability and unstable emotional state of the average elephant, it was felt that even with the keeper inside the chamber with the elephant, an "emergency exit," so to speak, was needed. Fortunately, however, an emergency opening of the door was never necessary. Although the outside dimensions of the southwest, open end of the chamber were 3 by 3 meters, obviously the smallest opening consistent with the size of the elephant was desirable if the door was to be removed and replaced without too great difficulty. Hence this 3 by 3 meter end was finally reduced until the door opening was actually only about 2.5 by 3 meters. The door was, therefore, light enough in weight so that three men could easily handle it. When removed from the chamber, it was leaned against the wall of the barn in the rear of the animal.

Position of elephant inside chamber—The elephant was led into the chamber and chained in position with her head at the end away from the door. It was feared that if she faced the door she might, through her natural curiosity, feel around it with her trunk, and that in case of leakage of air around the door some of her carbon-dioxide output might be lost with each expiration. Since a satisfactorily tight closure of the door was secured with the adhesive tape, this objection to having her face the door was overcome. But another reason for having her back toward the door was to facilitate the removal of feces after the experiment, in case feces were passed during the test. From the standpoint of the animal, however, it would have been better to have Jap face the door. It was necessary to put the door on (sliding it from the side rather than bringing it up from the back) and take it off several times before the elephant, with her back to the door, became adjusted to her environment. (See page 75.) Elephants' heads do not turn easily, elephants do not like to have anything going on behind them, and *anything new* tends to cause apprehension and inquietude. We certainly would recommend facing the elephant toward the door in any repetition of the experiments. When Jap came out of the chamber, she turned around inside the chamber first and was not backed out. In the original design of the apparatus the question of turning the elephant around inside the chamber did not come up. This proved to be essential, however, and it is fortunate that the chamber was built large enough to take care of this unanticipated problem.

Accessories in interior of chamber—To insure complete stirring of the air in the chamber and to have as little stratification of the air as possible, a small electric fan of not particularly great velocity was placed in the upper, rear corner of the chamber, near the ceiling. The direction of the air whirl was away from the door, to avoid having a blast of air against any possible pinholes or leakages around the door. An electric-light socket in the ceiling was provided with two bulbs, the second to be used in case the first burned out, thus avoiding leaving the keeper in total darkness with the elephant. (See figs. 1 and 2.) A small amount of light was also admitted by the window in the door. During the experiments the light was left on, and the fan was going the entire time. The keeper sat directly under the electric light in a chair near one of the rear legs of the elephant, close to the aperture A (Plates 2B and 4) with the rubber diaphragm covering, which was used for the speaking tube. To aid in controlling the activities of the elephant and to prevent any contact with the sides of the chamber, two eye bolts (k, Plate 3A) were suitably placed in the floor so that she could be chained at the front and rear.

Ventilation System

The ventilation principle used was one that has been employed for many years at the Nutrition Laboratory, that is, to select first a respiration chamber of suitable size for the particular animal to be studied, to connect this chamber with a supply of pure outdoor air, to withdraw air from the chamber by a blower at a rate such that the outcoming chamber air will have a carbon-dioxide content of about one per cent, to meter this current of air, usually with a dry gas meter, and to make suitable provision for adequately aliquoting it. This whole principle is shown in the schematic drawing in figure 2. The elephant was inside the chamber and uncontaminated outdoor air entered through the pipe a (see also Plates 2B and 4 and fig. 1). Air was withdrawn near the top of the chamber through the pipe b, b, by means of blowers in the blower box B. These blowers discharged the air into the pipe c connecting with the dry gas meter M. Dry bulb thermometers, T_1 and T_2, and a wet bulb thermometer, T_3, recorded the temperature of the air before and after its passage through the meter. A small flow meter, R, indicated the rate of ventilation. Aliquot samples of the outcoming air current were collected in the unique sampling device, F, F, the so-called "Fox bags,"[1] and there was provision for bathing these bags with air leaving the meter through the pipe e and the rotary blower f, which forced the air through the pipe g, g, into the boxes containing the bags, F, F. The details of this ventilating system may be considered under the heads of introduction of outdoor air, removal of air from the chamber, blowers, meter, and aliquoting device.

INGOING AIR

Outdoor air was introduced by cutting a 10-cm. hole in the lower, right-hand corner of the door (see a, Plates 2B and 4 and fig. 1), and inserting in it a 10-cm. pipe with one end properly fitted to the door and the other end sticking out through the wall of the barn. Thus if there was a slight negative pressure inside the chamber, air from outside

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[1] Devised by the late Edward L. Fox of the Nutrition Laboratory staff.

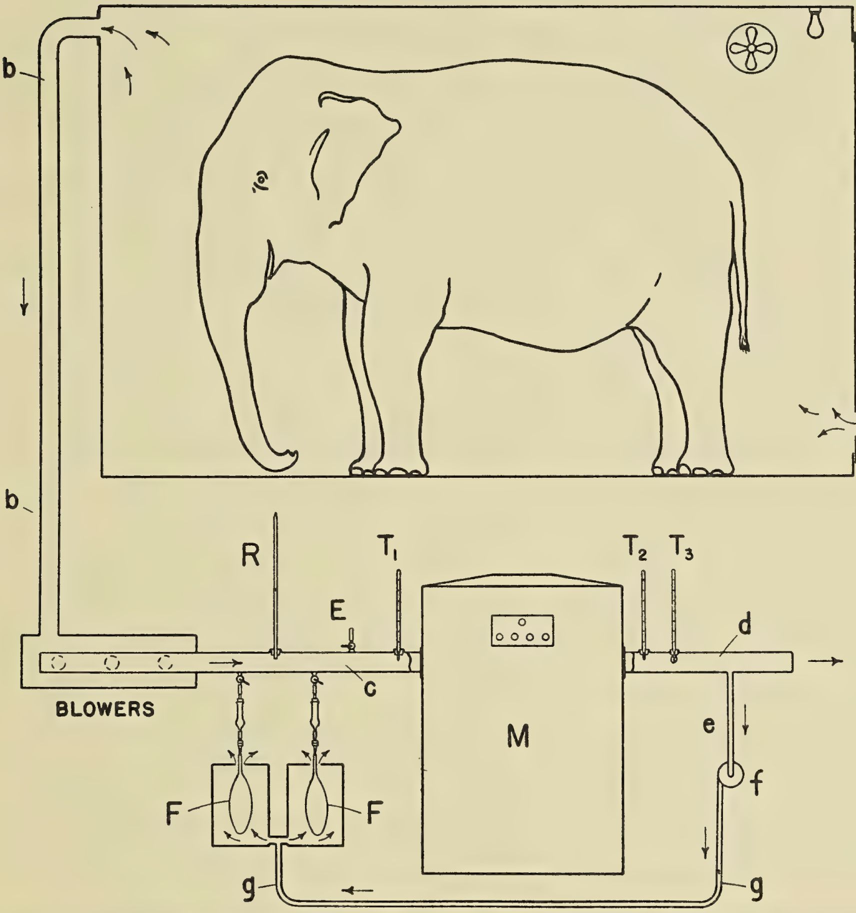

FIG. 2—DIAGRAM OF VENTILATING, ALIQUOTING, AND METERING SYSTEMS OF RESPIRATION CHAMBER.

a, pipe for introduction of outdoor air; b, b, pipe for outcoming chamber air; c, pipe connecting blower box with meter M; R, rotamesser indicating rate of ventilation; F, F, rubber bags for collection of samples of outcoming chamber air; T_1 and T_2, dry bulb thermometers; T_3, wet bulb thermometer; d, pipe for discharge of air from meter through wall of barn outdoors; e, pipe connecting with small blower, f, which forced portion of air discharged from meter through the pipe g, g, into boxes enclosing sampling bags; E, petcock for attachment of sampling pump.

could flow through the 10-cm. hole to equalize the pressure. With an adequately tight chamber, sufficient decrease in pressure could be obtained to allow enough outdoor air for the elephant to flow through this opening without any supplementary blowers in the nature of a forced draft. This method of relying upon a decrease in pressure to have the air flow in from outside assumes that the chamber is air-tight and that the only place where air can enter is through the 10-cm. pipe. These conditions must exist when the chamber is installed in a building where contaminated outdoor air might leak into an opening. This danger from contaminated air played only a small rôle in the elephant chamber for, if any leaks occurred, the air entering through these leaks in addition to that entering through the 10-cm. pipe would be barn air. From the nature of the open construction of the barn with its large, none too well-fitting doors (frequently open during experiments) and ample opportunity for air to enter the barn at different points, the respiration chamber was built practically in the equivalent of outdoor air. The only possible sources of contamination to any air that might leak into the chamber from the barn would be that supplied by the respiratory processes of the three or four observers and the possibility of leakage of carbon dioxide from the small stove used to take the chill off the air of the barn. However, the greatest percentage of the air entering the chamber must have been outdoor air, which entered through the 10-cm. air pipe, and we had to deal only with the theoretically possible error that might prevail due to the relatively small amount of air that could leak in the very few crevices around the door or other parts of the chamber that were not hermetically sealed. As will be seen later (page 53), this theoretically possible source of contamination of the air was proved by carbon-dioxide control tests not to be present in this apparatus in measurable amounts. But if this method of introducing outdoor air were to be used in a laboratory building, and especially in an animal house in a zoological park, obviously greatest precaution would have to be taken to insure complete absence of leaks, for the air surrounding the chamber and which might leak into it might be considerably contaminated by the heating plant or the carbon-dioxide production of other animals, assistants, and particularly the numerous visitors common in zoological parks.

REMOVAL OF AIR FROM CHAMBER

Blowers—From previous experience with other animals, it was realized that the elephant chamber must be ventilated at a rate such that the outdoor air in its passage through the chamber would be changed by the physiological processes of the elephant from a composition of 20.940 per cent oxygen and 0.030 per cent carbon dioxide to a composition, as the air left the chamber, of approximately 1 per cent carbon dioxide and not far from 19.90 per cent oxygen. A carbon-dioxide content of chamber air of 1 per cent is desirable for accurate gas analysis, and it has been demonstrated that this amount of carbon dioxide does not stimulate the respiratory center of an animal or man or affect in the slightest normal respiration. Calculation of the probable carbon-dioxide production of the elephant was, therefore, made, based upon its body weight and previous measurements on a 700-kg. Percheron horse, the largest animal upon which we had made measurements previous to the elephant study. This calculation indicated that the elephant might have a carbon-dioxide production of about 15 liters per minute. Rough calculations based on the daily consumption of hay and its estimated digestibility also suggested that the carbon-dioxide output would be about 15 liters per minute. On this basis it would be necessary to withdraw air from the elephant chamber at a rate of about 1500 liters per minute, in order not to have the carbon-dioxide content of the outcoming air exceed 1 per cent. With the large respiration chamber at Durham, New Hampshire, the most rapid ventilation rate ever used was 400 liters per minute. To remove air at a rate of 1500 liters per minute called for a combination of blowing devices that had not previously been developed at the Nutrition Laboratory. At Durham a vacuum cleaner motor had been used, enabling a ventilation rate of at least 600 liters per minute. For the elephant, therefore, it was planned to have three such blowers in parallel, so that a ventilation rate of at least 1800 liters per minute would be possible. In its ordinary household use, a vacuum cleaner is constructed to pull a large volume of air without any appreciable resistance to suction. This volume of air is discharged into a bag which, however, builds up considerable pressure against which the blower normally works. In our use of the instrument at Durham the air is discharged, at a maximum pressure of 3.5 cm. of water, into two standard, bellows type, dry gas meters in series. Although doubtless most, if not all, of the various vacuum cleaners would serve this purpose, the particular instrument used for ventilating the elephant chamber was one sold under the name of "Air Way" vacuum cleaner. This consists of a high-speed, universal motor, well mounted in an aluminum housing, with an aluminum fan. At Durham these motors had run at somewhat less than maximum speed for experiments of many consecutive days' duration. Hence, although normally designed for short intervals of service in household use, this motor, when not overloaded, will run perfectly for days at a time. Three of these motors were used for the elephant chamber. It was soon found that a ventilation rate of not far from 1500 to 1600 liters per minute could be secured by using only two of the three blowers, without overloading the motors. Hence the third blower was saved as a reserve in case one burned out. It could be put into service, if needed, during an experiment without opening the system, but it was not necessary to make use of this reserve blower.

Blower box—The blowers were mounted for accessibility in an air-tight, sheet metal box, with internal dimensions of 65.7 cm. in length, 26.5 cm. in width, and 19 cm. in depth. Each blower and motor was supplied with an independent electric connection, and each had its independent external resistance outside the box. Thus their speeds could be varied at will. The disposition of the blowers in their housing box is shown in Plate 5. Each blower, B_1, B_2, and B_3, was mounted in a wooden cradle attached to a wooden base, clamped, and strongly wired into place. The arrows indicate the direction of the air current. At the discharge ends of the blowers, tubes were soldered through the side of the box. Each of these tubes finally entered a 7.5-cm. metallic tube, c, one end of which was closed and the other end led directly into the metering device. The housing box for the blowers was supplied with a water seal, w, but throughout the entire experimental study of the elephant it was not once necessary to remove the cover for repairs or adjustments of the blowers. The water seal was 65 mm. deep and 30 mm. wide (internal dimensions). The blower box was provided with a metallic cover having a 7.5 cm. hole in the top approximately over the blower B_1. This hole connected directly with the vertical pipe b, b (fig. 2 and Plate 6) having two elbows at the top, which connected with the opening leading out from the top of the respiration chamber at the point indicated by the arrow in the upper left-hand corner of Plate 3A. This pipe b, b, was relatively short in length and offered no appreciable resistance. All joints between the blower box and this connecting air pipe b, b, and the connections with the three outgoing tubes to the outgoing air pipe, c, were of telescope fit, supplemented by taping with adhesive tape. The joints were, therefore, excellent, rapidly removable, and air-tight. The construction of the blower box, the mounting of the blowers, and the adjustment of supplementary valves and tubing were carried out by Mr. V. Coropatchinsky, mechanician of the Nutrition Laboratory.

Control of speed of ventilation—Most of the control of the speed of ventilation could be obtained by use of three independent external resistances. The leads to these external resistances are lettered s in Plate 5. A further control of the ventilating speed of each blower was obtained by operation of the butterfly valves, v_1, v_2, and v_3, in the discharge ends of the blowers. In actual experimenting, blowers B_1 and B_3 alone were used, and the butterfly valve v_2 of blower B_2 was closed to prevent blower B_2 from serving as a by-pass. The ventilation rate thus obtained could be reduced simply by opening valve v_2. Further reduction could have been obtained by closing either or both of the valves v_1 and v_3. With this combination of blowers and valves, any desired rate of ventilation within a great range could be secured without overloading the motors, one blower being held for reserve. When large volumes of air are to be removed, this ventilating apparatus can hardly be bettered for effectiveness and continuity of operation. The fact that the motors on the blowers are universal makes the use of the ventilation system practically universal. The blower system was so uniform in its function that the rate of ventilation per half hour (the ordinary length of the experimental period), after once established, was remarkably constant, rarely varying more than a fraction of a per cent. Hence no regulation of the blower system was necessary at any time after the initial establishment of the rate.

Measurement of Volume of Air Passing Through the System

METER

Measurement with an open-circuit chamber of the metabolism of an animal the size of an elephant requires not only precise gas analysis of the outcoming chamber air but the accurate measurement of the total volume of air leaving the chamber. The Nutrition Laboratory had developed a special aliquoting device[1] for measuring large volumes of air, but this had been

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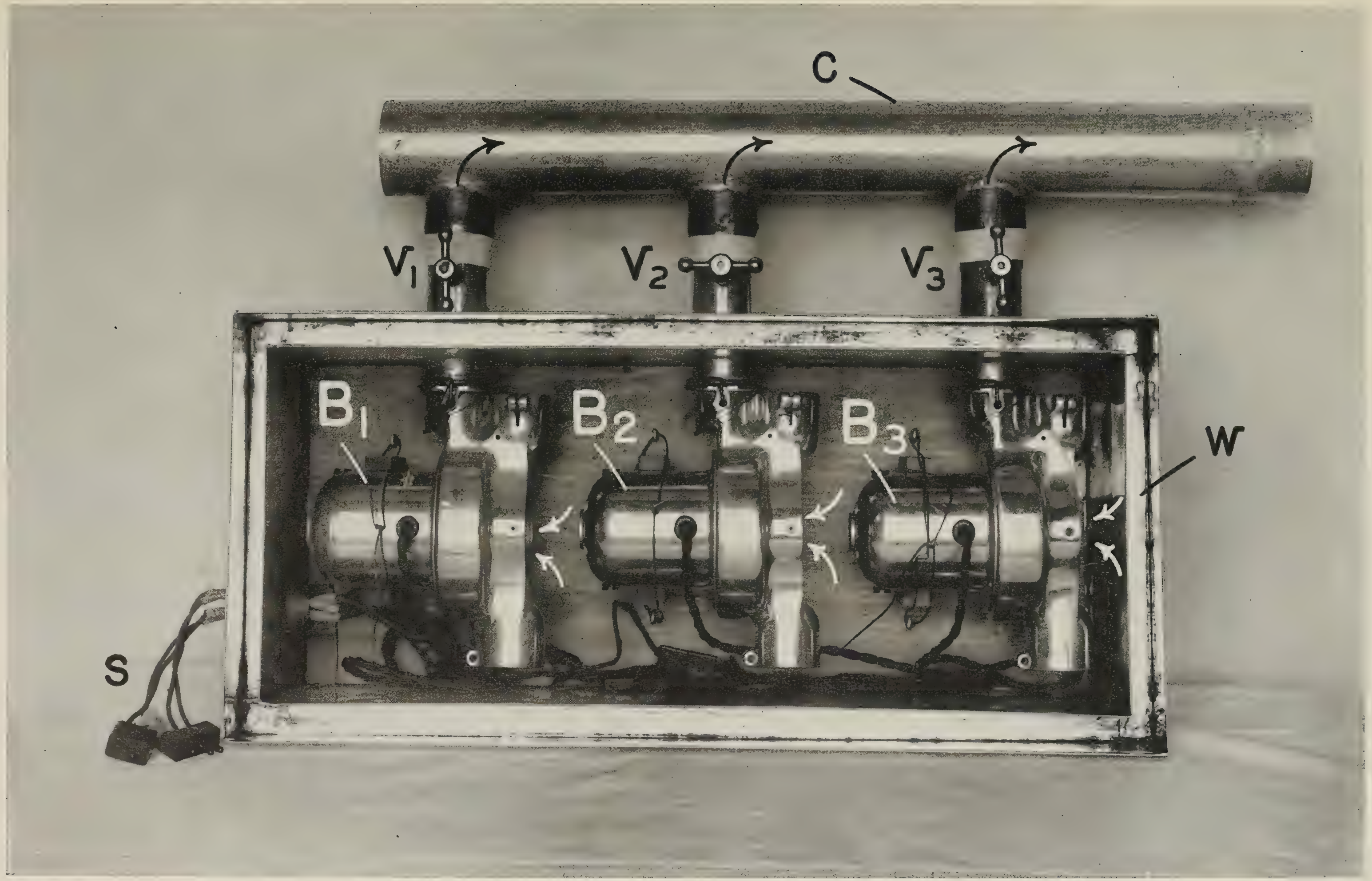
[1] Benedict, F. G., Abderhalden's Handb. d. biol. Arbeitsmethoden, 1924, Abt. IV, Teil 10, fig. 224, p. 547.



BLOWERS AND BLOWER BOX WITH COVER REMOVED

B_1, B_2, and B_3, vacuum cleaner blowers; w, water seal in the box housing the blowers; s, leads to external resistances (i, Plate 6) controlling speed of blowers; v_1, v_2, and v_3, butterfly valves also aiding in control of speed of blowers; c, pipe connecting blower box with metering and aliquoting systems. Arrows indicate direction of air current.

to a certain extent superseded by the use of dry gas meters. At Durham, New Hampshire, where a maximum ventilation rate of from 400 to 600 liters of air per minute had been measured, two dry gas meters in tandem had been successfully employed. The use, for accurate physiological measurements, of that industrial appliance, the dry gas meter (commonly employed for measuring household gas consumption), has always necessitated a pair of gas meters in tandem, on the sound principle that it would be impossible for two gas meters to become defective at precisely the same time and with the same degree of error. Hence if two dry gas meters are connected in tandem and calibrated by passing known amounts of air through them, the slight correction factor for each meter will be known and, what is more important, there will be a definite ratio between the differential readings by the two meters. As long as this ratio remains constant, it can be assumed that neither meter is inaccurate and the calculations based upon the meter readings are true. In many years of experience with dry gas meters of various sizes from as small as the ordinary 3-light gas meter to as large as the 60-light gas meter used at Durham, the Nutrition Laboratory has found that the ratio between the readings by any two gas meters remains extraordinarily uniform and that these meters can be used for two or more years before a significant error appears. It can, therefore, be assumed that the dry gas meter is an instrument of precision. This does not imply that the control of having two meters in series is not highly desirable. In fact, it is imperative in most work.

However, one large dry gas meter only, without a control, was used for measuring the volume of air leaving the elephant chamber. Since the meter was to be employed at the most for only a few days, since the expense of a gas meter is fairly considerable, and it would be unnecessary for the Nutrition Laboratory to use such a meter in subsequent researches, two meters seemed unjustifiable. A visit to the Cambridge Gas Light Company and consultation with the engineer, W. B. Morey, led to the conviction that a standard 150-light meter would measure volumes of air as great as necessary in the use of the elephant chamber without significant error other than the standard calibration factor. A meter of this size is an unwieldy instrument, and it was out of the question to think of transporting two such huge instruments. It was believed that in all probability careful observation and control of one meter would suffice. Through the courtesy of the Cambridge Gas Light Company we were allowed to use one of their meters of this size without charge. The meter registered in cubic feet and had six dials, on which seven figures to the left of the decimal point were read. The smallest dial had one complete revolution for each 100 cubic feet. Each subdivision of this dial was 10 cubic feet, but an estimate could easily be made to 1 cubic foot. We are grateful to Mr. G. G. Howie of this company for his invaluable courtesy and kindness in making this test possible and to Mr. W. B. Morey, the engineer, who provided us with the calibration factor (1.01). This correction factor, which unquestionably is of sufficient accuracy in industrial purposes, was checked by tests at the Nutrition Laboratory, where the meter was shipped. Here there were a large number of 3-light gas meters that had been carefully calibrated by the method of admitting oxygen through them from a previously weighed cylinder, noting the change in weight of the cylinder, and comparing the known volume of oxygen admitted with the volume recorded by the meter. One of these previously calibrated 3-light gas meters was connected with the large gas meter and air was passed through both meters for several hours. The total volume recorded by the 150-light meter agreed well with that recorded by the 3-light gas meter. In this test it was impossible to pass air through the meters at as fast a rate as would be the case in ordinary use, but since the calibration factor (1.01) for the large meter as established by the Cambridge Gas Light Company agreed with the calibration factor established in this comparison test with the 3-light meter, this was believed to be a satisfactory control. This correction factor meant that the readings on the large meter must be multiplied by 1.01 up to the rate of 3000 cubic feet per hour, to obtain the true reading. Since the ventilation rate used in the elephant measurements was about 50 cubic feet (1400 liters) per minute, it was justifiable to use this correction factor.

This meter was 114 cm. high, 81 cm. wide, and 61 cm. deep. This large, cumbersome instrument had to be delicately handled, and careful packing was necessary for its transportation by express from Boston to Campgaw, New Jersey. To protect it, the meter was heavily crated and securely attached to the crate to prevent any disturbance of its delicate mechanism, for the meter could not be easily calibrated again after being transported to Campgaw. In transportation, care was taken to keep the meter right side up, and the packing was such that the transportation company could not, without much trouble, lay the meter on its side. Although a second calibration of the meter was not made at Campgaw, the carbon-dioxide control test of the entire apparatus (which will be discussed later, page 54) served as an independent control not only of the whole equipment but also of the gas meter. The regularity of performance of the gas meter showed that no significant alteration in its mechanism took place during the ten days that it was used. Thus with a constant setting of the rheostats controlling the blowers and the blower valves, the number of cubic feet removed per hour from the chamber, as registered on the meter, was constant. When the meter was returned to the Cambridge Gas Light Company, it was examined carefully and no repairs or adjustments were found necessary. Furthermore, calibration of the meter upon its return showed that the correction factor was the same within half of a per cent as when it was first sent to us, having changed only from 1.01 to 1.005. A minor change from the original calibration is to be expected simply as a result of handling. It is, therefore, believed that the measurements by this meter were accurate to well within 1 per cent.

Since the meter had a considerable amount of oil of strong odor in its base, as an essential part of its construction, a 7.6-cm. pipe (d, fig. 2) was used to conduct the air from the meter out through a hole in the barn, without introducing any significant resistance to the meter.

Ideal conditions did not exist in the barn, for the meter had to be fairly near the stove used to take the chill from the air. This little stove was inadequate to make any accurate temperature control possible. About all it did was to make the extremely cold barn air slightly more comfortable for the operators. And yet the temperature of the environment near the stove was higher by several degrees than the temperature of the air in any other part of the barn. Although it was believed that accurate temperature readings of the wet and dry bulb thermometers (T_1, T_2, and T_3, fig. 2) would furnish data for reduction of the meter readings to 0° C., dry, and 760 mm., nevertheless this disadvantageous location of the meter was an important factor in emphasizing the necessity for a control of the accuracy of the entire equipment by a carbon-dioxide control test. The warmth from the stove was an advantage from one standpoint, however. The rate of ventilation of the chamber was hardly rapid enough to remove completely the water vapor given off by the animal without condensation in the air pipes b and c and the meter, but the warming of the meter by the stove to a temperature above that of the air entering the meter prevented any condensation of moisture inside the meter.

ROTAMESSER

A fairly accurate test of the rate of ventilation was provided by attaching to the air pipe c, before it entered the meter M (fig. 2), a small flow meter, R, a so-called "rotamesser." This instrument should be far more generally used in laboratories and is well worth a few words of description. It is furnished by the Deutsche Rotawerke of Aachen, Germany. It consists of a glass tube slightly tapered inside, with the larger opening at the top. Suspended in the current of air passing through this tube is a cylindrical bit of hard rubber, small enough not to touch the glass sides of the tube and yet of a size sufficient to close it almost completely when it is at the bottom of the tube. The greater the flow of air through the tube, the higher is this rubber float raised as the air escapes around the float and up the walls of the tube. Small grooves in the float cause it to spin rapidly while suspended in the upward moving air current and thus eliminate any friction caused by contact with the wall of the tube. A large number of these instruments of various sizes have been tested at the Nutrition Laboratory and have been shown to be extraördinarily accurate. A calibration curve is necessary when extreme accuracy is desired, but according to the calibration curve the correction factor does not change for any given air discharge. The great advantage of the rotamesser is that one can see instantly by the height of suspension of the float whether the rate of passage of air is constant or not. The rotamesser placed in the tube c was provided, at the top, with a capillary jet. Thus the volume of chamber air escaping through the rotamesser and hence not measured by the meter M was reduced to approximately 1 liter per minute, a negligible percentage of the total volume of outgoing air.

In the respiration experiments with the elephant it so happened, not by design, that the float of the rotamesser was suspended at a height corresponding closely (when interpreted in terms of volume of flow per minute) to the number of cubic feet discharged per minute through the meter. The float bobbed up and down, due to the bellows effect inside the meter, but the maximum height of suspension of the float during any one period of the bellows movement always corresponded closely to the cubic feet of air discharged per minute. In the installation of the various parts of the ventilating apparatus it was necessary to place the gas meter with its dial next to the wall of the barn, where it was not immediately readable from the front of the apparatus. The rotamesser, however, instantly indicated the rate of flow of the air current at any moment during the period of measurement. Indeed, the rotamesser was extremely helpful on many occasions in indicating immediately the rate of ventilation, especially in starting the experimental period before the meter readings were compared with the time on a stopwatch.

The rotamesser float functions only when rotated in dry air. If moisture condenses on the glass tube, it often prevents rotation and correct suspension of the float. A drying tube containing calcium chloride (not shown in fig. 2) was, therefore, placed between the rotamesser and the pipe c.

Aliquoting of Ventilating Air Current

After the satisfactory construction of the respiration chamber and the installation of a most efficient ventilating blower system and an accurate metering device, the suitable aliquoting of the outcoming chamber air was of paramount importance. It was believed that experiments of less than one-half hour would not be satisfactory. Consequently it became essential to obtain a sample of suitable size for gas analysis that would be truly representative of the total discharge from the respiration chamber during 30 minutes, a discharge at the rate of 1500 liters per minute. A method was devised whereby a very small fraction of the total ventilating air current was collected for this purpose. In the course of the Nutrition Laboratory's experiments with men and animals, numerous aliquoting devices have been used from time to time. Many of these were obviously unfitted for the problem at hand, but finally one was decided upon that had been the most universally applicable and had been actually used in the Laboratory in measurements of the metabolism of animals ranging in size from as small as a 20-gram mouse to as large as a 700-kg. horse. This particular principle, although employed a great deal at the Nutrition Laboratory, has been only inadequately described, and the following description is given in response to the requests of research workers interested in this type of aliquoting. The method was developed by our late associate, Mr. Edward L. Fox. It has been mentioned frequently in lectures before European audiences and was first illustrated in a pamphlet describing the work of the Nutrition Laboratory and the Carnegie Institution of Washington in general in 1927.[1] The entire apparatus was shown to the members of the XIIIth International Physiological Congress in Boston, August 19 to 24, 1929. A brief description of it was published by Carpenter and Fox in 1931.[2]

The "Fox bag," as it is colloquially termed, is a rubber bag that can be attached to the main ventilating air current on any form of respiration chamber to collect continuously a proportionate fraction (dry) of the air leaving the chamber. By means of a very small opening, either a capillary tube or a disk with a hole in it, a portion of the outcoming chamber air is allowed to pass slowly but continuously into this bag as a result of the pressure in the main air-current pipe. With a relatively constant pressure, the volume of air passing into the bag will always be the same proportion of the total ventilating air current. Specifically in the case of the elephant chamber (fig. 2) throughout the period of measurement, a small fraction of the air coming from the discharge of the blower box, which connected directly with the pipe c, was forced into the bag by pressure through a jet provided with a small orifice. Two of these bags were used in the elephant apparatus, as shown by F, F, in figure 2. The duplicate use of the Fox bag is also seen in Plate 6 (page 56), although in this illustration the position of the bags and the jets is imperfectly shown. The details of the arrangement of the bag and jet are given in figure 3. The air from the blowers was discharged into the pipe c. Onto this pipe was soldered a petcock, H. This in turn was connected with a small calcium-chloride tube G, below which was a brass union in which was a small disk, an enlargement of which, D, is shown at the right side of the drawing. In the center of this disk was a microscopic hole. The jet was tapered at its lower end, and the neck of the rubber bag F fitted over this tapered end. These bags are the 4-piece, stem type of bladder used for the interior of basketballs. The gusset-type, seamed-edge bag shown in dotted outline in figure 3 permitted all the air to be expelled

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[1] Illustrated pamphlet of the Carnegie Institution of Washington, 13th ed., 1927.

[2] Carpenter, T. M., and E. L. Fox, Arbeitsphysiologie, 1931, 4, p. 527.

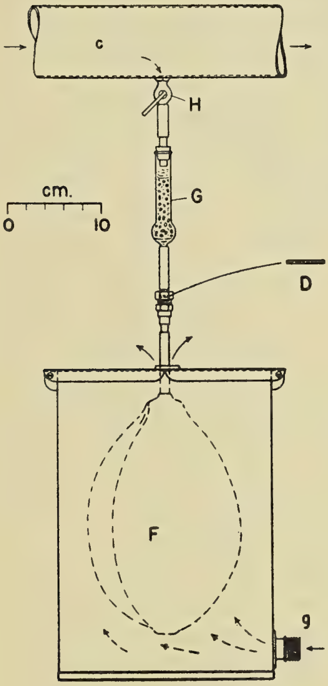

Fig. 3—The "Fox bag" for collection of an aliquot sample of air coming from an open-circuit respiration chamber.

Throughout the period of measurement a portion of the outcoming chamber air passing through the pipe c (connecting blower box and dry gas meter) escapes through the petcock H, through the tube of calcium chloride, G (where the water vapor is removed), and through a small opening in the disk D, into the Fox bag, F. Some of the outcoming chamber air, after it is discharged through the dry gas meter, is diverted through the pipe g into the box containing the Fox bag and escapes through an opening in the center of the top of the box.

from it when it was laid flat on its side and likewise presented minimum resistance as the air entered the bag. Under these conditions a small portion of air continually left the pipe c through the petcock H, passed through the calcium chloride in the tube G, where it was thoroughly dried, then through the small hole in the disk D and through the tapered end of the jet into the bag F. At the bottom of the calcium-chloride tube sufficient cotton batting was placed to insure absence of dust in the air when it entered the orifice in the disk. Removal of water from the air was essential to enable 24-hour storage of the sample, if necessary, without change in chemical composition. Drying of the air sample was likewise desirable, as otherwise the orifice might have been closed by a drop of water condensing there. The calcium chloride in this tube was changed before nearly every respiration experiment. In experiments with a high ventilation rate, the pressure at the jet was reduced by partly closing the petcock H.

Air-bathing principle—By reason of the fundamental principles of the ventilating system of an open-circuit respiration chamber of this type, the air collected inside the Fox bag will contain from about 0.7 to 1.1 per cent carbon dioxide. When this bag is hanging freely in a room or barn, it is surrounded by air containing at the most 0.050 per cent and probably more nearly 0.030 per cent carbon dioxide. Under these conditions diffusion of carbon dioxide out of the bag certainly would take place during half an hour. To avoid this, the Fox bag is hung freely in a small metallic box of such size that when the bag is distended to its normal size, it does not come in contact with the sides of the box. By furnishing this box with air through the pipe g from the discharge side of the meter M (fig. 2), the bag F was, throughout the entire period of collection of the air sample, bathed with air of approximately the same chemical composition as that inside the bag, and no change in the composition of the air sample took place by diffusion either into or out of the bag. In this particular case, instead of trying to lead air directly from the discharge of the meter, it was simpler to use a small supplementary blower, f (fig. 2), to draw the air from the discharge pipe d into the pipe e and thence force it into the pipe g and into the bottom of the two boxes in which the rubber bags F and F were suspended. The air entering the bottoms of the boxes rose around the outside of the bags and escaped through the narrow orifices where the rubber necks of the bags passed through the tops of the boxes. The top of each box (fig. 3) was built in two sections, in the form of hinged covers which could be lifted rapidly at the end of each experimental period to allow quick withdrawal of the bag and replacement with another, deflated bag. Under these conditions and since the metabolism of the elephant remained essentially unaltered throughout the several half-hour periods of the experiment, each bag was continually bathed on the outside by air of essentially the same composition as that of the air inside. Although this air-bathing principle functions perfectly in a 10- or 12-minute experiment with man and in half-hour experiments with sheep and other animals, the Nutrition

Laboratory has not thought it advisable to employ this method when there is to be a collection of gas over many hours, for example, in a 12-hour period with a large ruminant. For this purpose, in place of the rubber bag, a delicately counterpoised spirometer is employed. The outside of this spirometer also is bathed with air of the same composition as the air collected inside.[1]

Uniformity of aliquoting—Given an orifice of a certain cross-section, the amount of gas flowing through it will be dependent upon the pressure, provided there is no external resistance to the flow of gas. It is true that, theoretically at least, the resistance presented by the bag will gradually increase as the bag becomes distended. If the bag is allowed to become too distended, then the true aliquoting will be disturbed, for as the bag fills with gas and the pressure inside the bag increases, proportionately less of the outcoming chamber air will be delivered into it. This is particularly true of bags that depend on stretching of the rubber to obtain the desired volume. But with a bag constructed with folds and pleats this resistance begins at a minimum, being almost negligible, and only slowly increases sufficiently to present a real disturbance of the regularity of aliquoting. The rate of the total discharge of air from the chamber is dependent solely upon the efficiency of the blower and the pressure at which the air enters the meter. The Fox bag differs from the meter in this fundamental point. The meter has free discharge of air, but the air discharged into the Fox bag is, theoretically at least, under continually changing resistance. As the bag fills, the resistance becomes greater and greater, and hence air is passed through the disk into the bag under continually increasing back pressure. Consequently one would expect slightly more air to be discharged into the Fox bag during the first minute of a 30-minute period than during the last minute. A sufficient volume of sample can be obtained, however, so that it is unnecessary to fill the bag to the stretching point. Hence the resistance is practically only that required to support the unstretched walls of the bag, and it remains relatively constant. Until the bag is filled with 3 liters, a resistance of only 2 or 3 mm. of water pressure will be required, and this resistance will remain constant until it starts to build up against the stretch of the rubber. The bag, when fully distended, might hold 6 liters, but it is safe to fill it only to the point where it holds 3 liters.

It has been the custom at the Nutrition Laboratory in many of its animal studies to employ two Fox bags and thus have duplicate collections of aliquot samples. At the beginning of the metabolism measurements on the elephant, it was decided to rely upon two independent Fox bags, each with its aliquoting disk, because the tests were too important and too difficult of reproduction not to be sure of adequate sampling. It was soon found, however, that the samples collected in the two bags had invariably the same chemical composition and hence, because of the large amount of other work to be done, it was subsequently decided to use only one bag. As each day's experiment usually consisted of eight consecutive half-hour periods of measurement, in a sense these periods could be looked upon as controls of each other. For perfect aliquoting, it is essential that the sample be taken proportional to the total volume of air discharged. This is especially true when considerable variations in the carbon-dioxide production of an animal may be expected within a relatively short time, which (on the assumption that the ventilation rate is held constant) would result in a variation of the true percentage of carbon dioxide in the ventilating air current. The measurements on Jap showed that she gave off, on the whole, remarkably uniform amounts of carbon dioxide per half hour, and the extra precautions that were taken for perfect aliquoting were perhaps unnecessary.

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[1] Benedict, F. G., Coropatchinsky, V., and E. G. Ritzman, Abderhalden's Handb. d. biolog. Arbeitsmethoden, 1934, Abt. IV, Teil 13, p. 619.

Volume of aliquot sample—For the transport of the air samples from the rubber bags to the gas-analysis apparatus use was made of pumps. (See page 51.) To fill these pumps and properly wash out the dead space, it was essential to have the volume of the sample collected in the bag amount to at least 1 liter and preferably 1.5 liters. Consequently the optimum amount to be collected in a 30-minute period ranged from 1.5 to 3.0 liters. This was dependent upon the pressure in the air pipe c, on the one hand, and the size of the orifice in the disk D, on the other. Preliminary tests in Boston with various rates of flow with the particular meter employed with the elephant chamber suggested the correct size of the opening in the disk, which was found to be 0.5 mm. In the apparatus as finally set up at Campgaw there was, in the pipe c, a positive pressure of about 20 mm. of water, and this size of disk allowed a discharge of air into the Fox bag sufficient in volume for all purposes of sampling and washing out of the pumps. Since the amount collected in the Fox bag was such an insignificant percentage of the total volume of outcoming chamber air, no correction for the amount of sample collected was necessary in the calculation of results. Such a correction is highly important, however, when the total volume of outcoming chamber air is small, as would be the case in experiments with a rabbit or a rat. In these instances the actual amount collected in the bag should be added to the total metered volume.

At the end of the half-hour period of measurement, one of the Fox bags was removed and a second, which had been previously washed with air discharged from the meter, was hung in its place. Immediately after the bag was removed from its sampling jet, it was connected with a pump, and the dead space in the pump was washed two or three times with air from the bag. Finally the pump was filled with the sample, the stopcock on the bottom of the pump was turned, and the piston of the pump was pushed down as far as it would go under ordinary hand pressure, so as to leave the air in the pump under pressure. The sample was then carried safely to the temporary laboratory where the gas analyses were to be made. As a control of this whole method of sampling, a sampling pump (page 51) was connected with the petcock E (fig. 2) in the air pipe c and was thoroughly swept out with dry ventilating air. Starting with the beginning of the period, the piston was pulled out 3 mm. every half minute during the half-hour period, so that the pump was practically filled by the end of the 30-minute period. Comparison of the chemical composition of this sample with that of a sample simultaneously collected in the Fox bag invariably showed perfect agreement.

Residual Samples

With a respiration chamber of 43,000 liters capacity, the difference in the composition of the air at the beginning and the end of the period of measurement may be of sufficient magnitude to call for a correction of the carbon-dioxide production as calculated from the metered volume of outcoming chamber air and the results of the gas analysis. Since the ventilation rate was so high and since the method of determining the change in composition of the air residual in the chamber was to be a differential one, samples of chamber air could be taken at the beginning of the first period and just before the end of each succeeding period at a point in the system near that where the aliquot sample was collected, namely, through the petcock E (fig. 2) in the pipe c, between the blowers and the meter. The usual sampling pump was employed for this purpose. Just before the sample was drawn, the pump was thoroughly washed by drawing air from the ventilating air current through it several times and discharging it. The sample was then drawn, put under slight pressure, and set aside for subsequent analysis. Usually it was analyzed only for its carbon-dioxide content.

Analysis of Chamber Air Samples for Carbon Dioxide, Oxygen, Methane, and Water Vapor

GAS-ANALYSIS APPARATUS

No measurements made on the elephant compared in importance to those of the gaseous products of respiration, the oxygen consumption, and the production of carbon dioxide, methane, and water vapor. Fortunately, owing to the long experience of Dr. T. M. Carpenter in exact measurements of this kind, two forms of his precise gas-analysis apparatus were available, and these were an important part of the equipment at Campgaw. Two of these apparatus of the form permitting determinations of both oxygen and carbon dioxide and one of the form enabling methane determinations were employed. With these apparatus it is possible, in the case of air containing about 1 per cent carbon dioxide, to determine the carbon-dioxide content of air samples to within ± 0.003 per cent, and the oxygen and methane contents to within ± 0.005 per cent. With these two forms of the Carpenter apparatus and a moderate ventilation of the respiration chamber, one can be reasonably certain that the determinations of the carbon dioxide, oxygen, and methane in the outcoming chamber air are accurate to well within one per cent of the total. These highly perfected types of gas-analysis apparatus have been so fully described by Carpenter that reference only to the published descriptions is necessary here.[1]

CHEMICAL HYGROMETER

For study of the water-vapor output, a gaseous factor thus far usually neglected in studies of large animals, recourse may be had to the various types of wet and dry bulb thermometers; but for the elephant research, use was made of the chemical hygrometer developed by Dr. Carpenter and recently described by him.[2] This apparatus has been used and controlled with other methods at the Nutrition Laboratory and particularly at the University of New Hampshire, and control tests have shown that the apparatus functions perfectly. To measure the water-vapor output it was necessary to determine the humidity of the air leaving the chamber and also that of the air entering the chamber. Theoretically this latter determination should have been made at the point at which the air entered the chamber, that is, the southeast side of the barn. It was believed, however, that the long lead that would be necessary between this point of entrance and the Carpenter hygrometer might introduce an element of condensation. It was, therefore, assumed (since there was no visible condensation that would alter this assumption) that the percentage of moisture in the outdoor air was so evenly distributed that a sample drawn from outdoors near the blower box would be equally satisfactory. For this purpose a hole was bored through the wall of the barn and through this was led a 1.5-meter length of copper tubing about 3 mm. in internal diameter. This tubing was connected to the common side of a Y type stopcock. A small auxiliary blower of centrifugal type was connected to one arm of this stopcock. The second arm of the Y was connected to another 3-way stopcock used in the reverse position, which was attached to the hygrometer apparatus to permit sampling. The small blower sucked outdoor air through the pipe and through the first 3-way stopcock. This insured air of the composition of outdoor air being supplied to this point. To draw the sample into the hygrometer, the first stopcock was reversed and the mercury in the burette of the hygrometer was required to move the air, wash the apparatus, and fill it with the sample for analysis. For obtaining the sample of the ventilating air, a short connection direct from petcock E to the second stopcock was made and the sample drawn as before.

Particular precautions were also taken to have no condensation of moisture inside the chamber or in the pipes leading from the chamber to the meter. Although the chamber temperatures when the water-vapor determinations were made were between 23° and 25° C., the barn temperature was many degrees lower, which facilitated condensation in the ventilating air pipes. If the chamber were ventilated at a rate such that the carbon-dioxide percentage in the chamber air would be 1 per cent, there would not be enough air passing through the chamber to bring out completely all the water vaporized by the animal. This would be particularly true if the air entering the chamber were saturated with water vapor. To avoid this difficulty, the ventilation of the chamber was purposely increased to such a point that there was no visible condensation of water. In the earlier experiments with slower ventilation rate, invariably a liberal condensation of water was noted on the walls of the chamber, especially the lower half of the sides of the chamber. This did not appear when the ventilation rate was increased nearly 50 or 70 per cent, although under these conditions the ventilating air was not completely saturated. The more rapid ventilation rate in these water-vapor studies resulted in a carbon-dioxide content of the chamber air lower than 1 per cent, but not low enough to affect the accuracy of the determinations of the carbon-dioxide increment by the Carpenter gas-analysis apparatus.

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[1] Carpenter, T. M., Journ. Metab. Research, 1923, **4**, p. 1; Carpenter, T. M., and E. L. Fox, Journ. Biol. Chem., 1926, **70**, p. 115; Carpenter, T. M., Fox, E. L., and A. F. Sereque, Journ. Biol. Chem., 1929, **83**, p. 211; Carpenter, T. M., Lee, R. C., and A. E. Finnerty, Wiss. Arch. f. Landw., Abt. B., Tierernährung u. Tierzucht, 1930, **4**, p. 1; Carpenter, T. M., Abderhalden's Handb. d. biolog. Arbeitsmethoden, Abt. IV, Teil 13, 1933, p. 593; Carpenter, T. M., Journ. Biol. Chem., 1933, **101**, p. 595.

[2] Carpenter, T. M., Journ. Biol. Chem., 1935, **112**, p. 123.

GAS-ANALYSIS LABORATORY

The natural inquisitiveness and potential destructiveness of the elephant and the fact that the barn at Campgaw was inadequately heated and obviously contained no ordinary laboratory facilities made it inadvisable to install the elaborate gas-analysis equipment in the barn. Thanks to the kindness of Mr. J. Donald Bish, however, the equipment of four gas-analysis apparatus (including a small Haldane apparatus for use in the trunk-breathing experiments—see page 56) was installed in his office, in a building about 150 meters away from the elephant barn, well lighted by electricity and with excellently controlled steam heat, giving a very uniform temperature. Without this arrangement it would have been difficult to have made the gas analyses. The temperature of the barn was not only too cold for gas analyses (at temperatures below 15° C., which often prevailed in the barn, the absorption of oxygen by potassium pyrogallate in the apparatus is very slow) but underwent enormous fluctuations. Every time the stove was replenished with fuel the temperature rose. Every time the barn doors were opened the temperature fell, and the only doors in the barn for admission of attendants or keepers were those built large enough to allow the elephant herself to enter or leave. Subsequent experience showed that the installation of the gas-analysis apparatus in Mr. Bish's office was a particularly successful solution of a complicated problem.

SAMPLING PUMPS

For the transportation of the samples of chamber air to the gas-analysis laboratory it was not necessary to rely upon the usual gas samplers, either Haldane or Bailey, with their large amounts of mercury, but use was made of a sampling pump of metallic construction, simple in design, having the advantage of being accurate in delivery, air-tight, light in weight, and practically indestructible. This pump has found extensive use at the Nutrition Laboratory not only for holding samples but for metering the amounts of oxygen admitted to small respiration chambers such as those for rats, rabbits, doves, and mice. Previous tests have shown that when the pump is thoroughly *dry*, a sample of *dry* air can be retained in the pump under slight pressure for at least 24 hours with an alteration during this time of not more than ± 0.004 per cent in either the carbon dioxide or the oxygen content.[1] The sampling pump is shown at o, near the right-hand side of Plate 6. These pumps were of inestimable service to us. If we had had to run over from the barn to the gas-analysis laboratory, a distance of 150 meters, over muddy ground and in all kinds of weather, with mercury samplers containing from 2 to 3 kg. of mercury, all sorts of accidents might have occurred. But these pumps solved that problem and are strongly recommended. They present no danger of breakage, hold the samples well, and the composition of the air stored in them is not appreciably altered. Although all gas analyses were made within six hours after collection of the air samples, nevertheless it was reassuring to know that in case of emergency the pumps could be relied upon for 24-hour storage. Never before in the history of the Nutrition Laboratory had any sampling device been subjected to the strain experienced at Campgaw. Mercury and glass samplers would unquestionably have failed completely, with great loss of samples and mercury.

Measurement of Temperature of the Respiration Chamber

The temperature of the respiration chamber was unsatisfactorily recorded. Theoretically a series of thermometers should have been used in different parts of the chamber. The playful, rather destructive characteristics of the elephant, however, made it reasonably sure that she would try to play with and break any thermometer bulb she might see projecting through the chamber walls. Hence there was but one thermometer in the wall, near the top of the chamber not far from the outcoming air pipe. This thermometer indicated at least the relative differences in chamber temperature and probably not far from the average chamber temperature. To read this thermometer it was necessary to climb a ladder. Care was taken that the ladder did not strike against the frame of the chamber when the thermometer was read, but it was impossible to avoid making some noise.

Measurement of Temperature of Ventilating Air Current

There was also a dry bulb thermometer, T_1 (fig. 2), in the air pipe c just before the meter M. To reduce the volume of outcoming chamber air as measured on this gas meter to 0° C., dry, and 760 mm., it was essential to know the degree of saturation of the air passing through the meter. Hence on the exit side of the meter a dry and a wet bulb thermometer, T_2 and T_3, were used (also shown on the left-hand side of Plate 6 in the outgoing air pipe d). It was impracticable to employ a constant levelling device for the distilled water which would be required to keep the thermometer bulb wet in this pipe with the enormous ventilation used. Consequently the wet bulb thermometer, coated with fabric, was taken out of its tube before each temperature reading, dipped in a bottle of distilled water, and then put back into the tube. When the mercury in this thermometer reached its lowest point and remained constant at that point, readings were taken of both the dry and the wet bulb thermometers.

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[1] Lee, R. C., Indus. and Eng. Chem., Anal. Ed., 1933, 5, p. 354.

Control Tests of Respiration Apparatus

TEST FOR TIGHTNESS

During the period of construction of the respiration chamber and its connection with the ventilating device, it was constantly borne in mind that to be effective the chamber must be as nearly as possible air-tight. Ideally this was to be striven for. It was certain that, because of the inability to solder a huge box of this kind except at great expense and delay in using it, there would inevitably be some leaks, especially around the nail holes, that would not be easily accessible. By reason of the location of the apparatus in the large well-ventilated barn containing practically uncontaminated outdoor air, it was assumed that unless the leaks in the chamber were very great, no respiratory gases of the elephant would be lost from the chamber, provided a slightly decreased pressure was maintained in the chamber so that in case of any slight leaks air would pass from the outside in, rather than *vice versa.* Theoretically it is conceivable that the chamber could be constructed without the connecting air pipe (a, Plates 2B and 4 and figs. 1 and 2) and that an inflow of air sufficient to ventilate the chamber at the rate of 1600 liters per minute could take place through existing holes and seams in the chamber without detriment to the accuracy of functioning of the apparatus. However, as there were inevitably considerable differences in temperature between the top and bottom of the chamber and different movements of the air inside the chamber, there might have been a leakage of air *into* the chamber at one point and *out* of the chamber at another, unless there was a definitely decreased pressure in the chamber. The first test of the accuracy of functioning of the apparatus, therefore, was to determine whether a decreased pressure could be established inside the chamber by running the blowers at slow speed and what speed or volume of ventilation per minute was necessary to produce a significantly decreased pressure.

For this purpose a delicate Sondén manometer (a glass tube bent in an arc with a drop of kerosene oil in it—see z, Plate 6) was mounted on one of the outside walls of the chamber and connected with the inside of the chamber by means of rubber tubing and a small glass tube. The door was then put in place and taped as described on page 35. The 10-cm. pipe, a, in the door was inserted, the butterfly valve located in this pipe for other purposes (page 55) was closed, and a practically tight closure of the chamber (although by no means perfectly tight) was secured. The position of the oil bubble in the manometer was noted both before the blowers were started and while operating. At a ventilation rate of less than 40 cubic feet or 1200 liters, a definite decrease in the pressure of the chamber was observed. When the butterfly valve was fully opened and the blowers were increased in speed until 1500 liters of air per minute passed through the chamber, it was found that the chamber was so tight that there was *still* a definitely decreased pressure even though air was entering through pipe a, with full benefit of its 10-cm. diameter. This indicated that the large volume of air flowing into the chamber entered through the 10-cm. pipe a, and only an insignificant (but not measured and hence not actually demonstrated) amount leaked in from the barn. Hence it was argued that, provided the experiments were all made with a decreased pressure in the chamber, there could be no error in the measurement of the respiratory products, for any air that leaked into the chamber in addition to the outdoor air entering through the 10-cm. pipe would be barn air, which was not measurably different in composition from that of outdoor air. This test for tightness, therefore, showed that the apparatus was satisfactorily tight and that Engineer Ackerman's aim to construct a chamber sufficiently tight for our purpose had been accomplished.

CARBON-DIOXIDE CONTROL TEST

Although it might have been justifiable to have assumed from this test for tightness that no loss of respiratory products could take place in the apparatus, nevertheless, in accordance with the regular procedure of the Nutrition Laboratory, a critical test of the accuracy of functioning of the entire equipment was made by the usual carbon-dioxide control test. This consists in introducing a known amount of carbon dioxide into the chamber and attempting to recover it by the measuring process represented by the entire system. It serves as a control (1) of the suitable introduction into the chamber of uncontaminated outdoor air containing 0.030 per cent carbon dioxide, (2) of the satisfactory removal of air from the chamber, (3) of the perfection of the aliquoting system, (4) of the accurate metering of the total volume of air leaving the chamber, and (5), although only incidentally, of the accuracy of the gas-analysis apparatus. The accuracy of this latter apparatus, however, having been controlled for so many years at the Nutrition Laboratory, its perfection in functioning could not for a moment be doubted.

The ideal control test for respiration chambers of any type is to produce inside the chamber by artificial means a known amount of carbon dioxide corresponding to that which will be produced by the animal subsequently to be studied and to remove this same amount from the chamber. This has been done with practically all the respiration chambers developed at the Nutrition Laboratory by burning known amounts of ethyl alcohol, on the assumption that the burning of one gram of anhydrous ethyl alcohol results in the production of 1.911 grams of carbon dioxide and the absorption of 2.085 grams of oxygen. The perfect combustion of very large amounts of alcohol has been attempted in the case of the large respiration chamber at Durham, New Hampshire, by burning of alcohol in a Barthel burner in an amount equivalent to the heat produced by a large steer, and reasonably satisfactory results have been obtained. But to burn alcohol sufficient to result in the production of 15 liters of carbon dioxide per minute, the amount estimated to be produced by the elephant, was out of the question without the use of an elaborate alcohol lamp actuated by a compressed air blast to atomize the alcohol. This would have called for considerable time-consuming experimental testing. Consequently the procedure used for controlling the entire elephant apparatus was that which has been employed for many years by Professor Ernest G. Ritzman at the University of New Hampshire, namely, introducing into the chamber a known amount of carbon dioxide and then attempting to recover it. The introduction of 15 liters of carbon dioxide per minute into a respiration chamber the size of the elephant chamber necessitated the use of liquefied carbon dioxide. This can be obtained from various firms in trade. The cylinders of liquefied carbon dioxide such as we used contain from 2.5 to 10 kg. By weighing such a cylinder on scales before and after introduction of carbon dioxide into the chamber, the amount of carbon dioxide thus introduced can be easily determined.

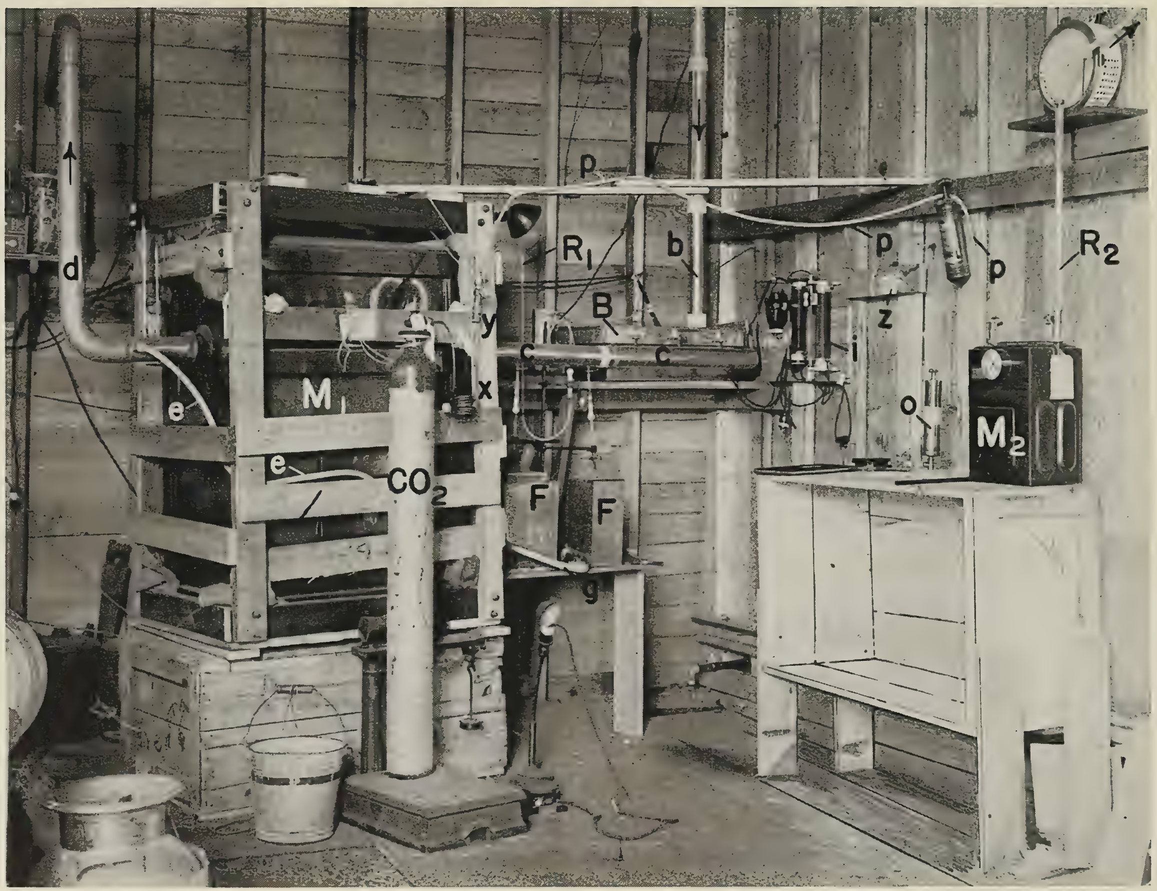
The arrangement for the carbon-dioxide control test of the elephant apparatus is shown in Plate 6. The liquefied carbon dioxide employed for this test was obtained from the Matheson Company at East Rutherford, New Jersey. We wish here to record our appreciation of the courtesy and care given to our problem, both by Mr. A. M. Matheson and his engineer, Mr. Dugan. Realizing that in the use of carbon dioxide from a high pressure cylinder there is always possibility of the gas solidifying on the needle valve controlling the flow of gas, Mr. Dugan kindly prepared a long coil of heavy copper tubing, x, to avoid this difficulty. This was immersed in hot water and thus the high pressure gas, before reaching the escape valve y, could be warmed up to 60° or 70° C. Under these conditions condensation of moisture in the valve and consequent stoppage of the valve did not take place. This equipment was sent gratuitously to Campgaw from the Matheson Company, and the cylinder of gas was placed upon the Fairbanks "silk" scale that was subsequently used for weighing feces and urine. In Plate 6 the cylinder of the gas is marked "CO_2."

As the immersion of the coil of pipe, x, in a pail of hot water complicated somewhat the process of weighing the carbon-dioxide cylinder and as there was available an accurate, previously calibrated dry gas meter, the carbon-dioxide cylinder was not weighed, but the carbon dioxide was metered by passing it through the dry gas meter M_2. The calculation of the results took account of the temperature of the carbon dioxide passing through this meter, the barometric pressure, and the fact that the carbon dioxide gas was dry. To aid in maintaining constant flow at the discharge of the meter M_2, a rotamesser, R_2 (see description on page 43), was attached to the exit side of the meter. This rotamesser was of large enough caliber to allow from 10 to 30 liters of gas to pass through it per minute. Thus it was unnecessary to attempt to count the revolutions of the meter M_2 as the gas was introduced, since the rotamesser indicated instantly whether the gas was being introduced at a constant rate. The gas left the cylinder through the rubber tubing p, p, p, passed through the meter M_2, the rotamesser R_2, and thence was conducted through a rubber tubing (attached to the top of the rotamesser) into the top of the chamber on the northwest side, at a point about half-way from the front to the rear. A thermometer in the exit side of the meter, just below the rotamesser, indicated the temperature of the gas.

To measure the total amount of carbon dioxide introduced into the chamber and especially to simulate the conditions under which the elephant was to be studied, it was necessary, first, to introduce into the chamber before the ventilation was started sufficient carbon dioxide to bring the percentage of that gas in the air of the chamber up to about 1 per cent. The ventilation of the chamber was, therefore, stopped, the butterfly valve in the incoming air pipe was closed to prevent any air from entering, and approximately 450 liters of carbon dioxide were rapidly introduced into the chamber from the cylinder. The total volume of the chamber being 43,000 liters, this procedure resulted in a carbon-dioxide content of about 1 per cent. The electric fan was allowed to run to stir the chamber air thoroughly. Shortly after the ventilation was started, a residual sample was drawn from the side of the chamber, readings were taken on both the large meter M_1 and the smaller meter M_2, and the time was recorded. Four consecutive periods, each of approximately 30-minutes' duration, were then made according to the procedure outlined on page 249, as in the regular respiration experiments. The carbon dioxide introduced during each period was measured simultaneously with the measurement of the recovered carbon dioxide, by reading of the meter M_2. At the end of the last period, that is, the end of the experiment, the flow of carbon dioxide from the cylinder was instantly stopped. Simultaneously the blowers were stopped, and a residual sample was drawn. This gave the data for determining whether there was any change in the amount of carbon dioxide residual in the chamber at the beginning and end of the test. The measurement by the metering, aliquoting, and gas-analysis apparatus of the carbon dioxide in the outcoming chamber air was corrected for any such change in residual carbon dioxide, and there was likewise a correction for the carbon dioxide in outdoor air. The whole procedure was simple and the recovery was complete. The average of several such half-hour test periods showed 100.2 per cent recovery.

Trunk-Breathing Appliance

Ideally the simplest procedure for measurement of the gaseous exchange of the elephant would be to place over the end of its trunk some sort of breathing appliance provided with inspiratory and expiratory valves, and to collect the expired air in a gigantic spirometer. From this spirometer a sample of the expired air could subsequently be withdrawn for gas analysis. Another possibility would be to employ a spirometer with a large carbon-dioxide absorbing system similar to the closed-circuit, spirometer types of respiration apparatus employed in the clinic, at the present day, in measurements on humans. In this case the spirometer need be of a size sufficient only to hold the maximum volume of an expiration and to permit the normal diminution in volume in the closed system due to a 6- or 8-minute absorption of oxygen by the animal. The use of a trunk-breathing appliance presents many problems, however. In the first place, there is the problem as to whether the temperamental, nervous elephant, whose trunk (particularly the tip end) is always in motion, will remain quiet enough while connected with such a breathing appliance for the 6- or 10-minute period needed in this type of experiment. Secondly, there is the problem of how to measure the volume of expired air, which may amount to 300 or 400 liters per minute in the case of the elephant. A spirometer of enormous size would be necessary for this purpose, and obviously complete collection by this means of the air expired during a 6- or 10-minute period is out of the question. In the third place, there is the serious challenge from the physiological standpoint as to whether the elephant breathes exclusively through its trunk or whether it can under any conditions breathe through its mouth. Since it is impossible



Arrangement for a carbon-dioxide control test of tightness and accuracy of functioning of the entire respiration apparatus.

Carbon dioxide under high pressure in a cylinder containing both liquid and gaseous carbon dioxide passed from the cylinder through coil of tubing x (immersed in hot water during test to prevent solidification of gas), through valve y, through rubber tubing p, p, p, through meter M_2, through rotamesser R_2, through tubing attached to top of this rotamesser, into top of respiration chamber. Air enriched with carbon dioxide left chamber through pipe b, and was forced by blowers in blower box B through pipe c, c, into meter M_1, from which it was discharged through pipe d to outside of barn. A portion of the air passing through pipe c, c, was collected in Fox bags for subsequent gas analysis. Some of air discharged into pipe d was drawn by a small blower (not visible in this photograph) through pipe e, e, and discharges through pipe g into the boxes F, F, holding the Fox bags. R_1, rotamesser indicating rate of ventilating air current leaving blower box; z, Sondén manometer to indicate whether there was a decreased pressure in the air inside chamber; i, external resistances controlling speed of blowers; o, sampling pump.

to make an air-tight closure of the elephant's mouth, as can be done with humans, the possibility of air passing through the mouth jeopardizes the accuracy of any measurements made with a trunk-breathing appliance.

Before we began our investigation, our friend Brody, of Missouri, had had the temerity to make experiments on trunk breathing alone and had reported in brief the results of his observations on three elephants, but with no description of the apparatus used.[1] Hence, although believing that the chamber method of measurement was by far the soundest physiologically, we thought it imperative to attempt some trunk-breathing experiments. The temperament of Jap was the first consideration, but her keeper assured us that she would consent to hold her trunk in some sort of mask. In the side of the large respiration chamber, about 75 cm. from the floor, was placed permanently a tube (A, Plate 2B) 18 cm. in internal diameter and 20 cm. long, in which a breathing appliance for the elephant's trunk could be supported more easily than by being held free in the air. This gave the advantage of having the trunk-breathing experiments made under the same conditions as the other respiration experiments, that is, with the elephant inside the chamber, although in the trunk-breathing experiments the animal was facing toward the door and the door was off. In the chamber respiration experiments with the chamber door closed, a metallic cap was telescoped over this 18-cm. tube and the joining made air-tight with adhesive tape. This cap had a hole in the center to which was soldered a projecting metal band or collar about 5 cm. in width. A piece of dental dam was stretched tightly over this hole and collar, and tied firmly with twine around the collar, to make a crude form of speaking tube. Since the keeper had his chair near this speaking tube, he had but to lean forward to speak readily to any one outside.

Respiratory mask—Of the various forms of mask considered, the one that seemed most promising (at that time we had no details of Brody's technique) was made from a 16-cm. galvanized iron tube, the diameter of which was based upon direct measurements of the diameter of the elephant's trunk at a point about 60 cm. from the tip. The edge of this pipe, where it fitted over the trunk, was well rolled and protected so it would not hurt the animal. Into this pipe (supported by the 18-cm. pipe A, as explained above) the elephant's trunk was thrust, and the junction between the trunk and the pipe was closed with automobile inner tubing, adhesive tape, and 3-inch rubber bandage. The contact of the tape with the trunk covered about six inches. An assistant also supported the pipe at this joining point. The details of this trunk-breathing appliance are shown in Plate 7. The end of the pipe L was closed with a telescopic fit by the cap n, and the joining was made air-tight with adhesive tape. The approximate position of the elephant's trunk inside the pipe is shown in dotted outline. The cap n was removed only during the period of training the elephant to the use of the breathing appliance, to reward her with a few lumps of sugar after she had placed her trunk in the pipe. Before the actual experiments, this cap was securely taped in place and thereafter not removed.

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[1] Brody, S., Procter, R. C., and U. S. Ashworth, Univ. Mo., Agric. Exper. Sta., Research Bull. 220, 1934. In the summer of 1935 Brody kindly sent us a complete description of his technique, with photographs, and the original curves drawn by his machine, which was a magnified form of the Nutrition Laboratory type of closed-circuit spirometer apparatus for graphic record of the oxygen consumption alone. A huge spirometer having a capacity of 663 cc. per millimeter length of bell was employed. A rubber sleeve was slipped over the elephant's trunk, and this was connected with the spirometer, which contained soda-lime for the absorption of carbon dioxide.

Expiratory and inspiratory valves—Because of the large volume of air discharged from the lungs of the elephant per minute and particularly the extraordinarily large volume during the brief interval (a second or so) of actual expiration, unusually large expiratory and inspiratory valves were necessary in this trunk-breathing appliance. In Plate 7 the inspiratory valve is lettered V_1 and the expiratory valve V_2. Each valve was in two parts, which fitted together telescope fashion and were closed air-tight by adhesive tape, t. The details of the construction of the valves are shown in figure 4. The design is simple. The air entered the bottom of the tube holding the valve, lifted an aluminum disk or plate, p, resting upon a sharp knife-edged ring, and flowed out through the top of the tube. To prevent the disk from being misplaced or driven up against the opening of the upper section of the valve, there were four upright brass guide rods, r, with rubber bands, h, stretched across their tops. Tests of these valves indicated that they were tight, light, rapid in action, and presented no appreciable resistance to breathing.

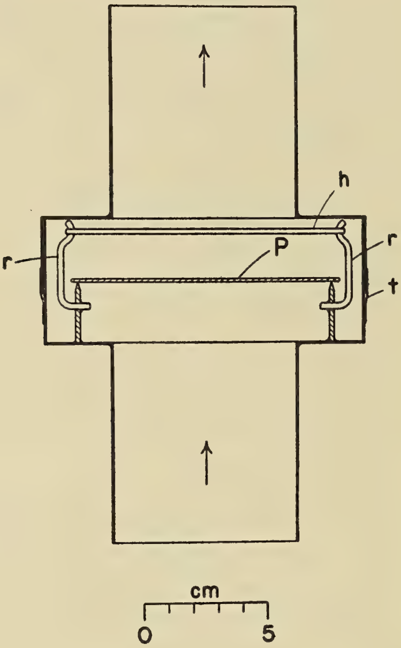
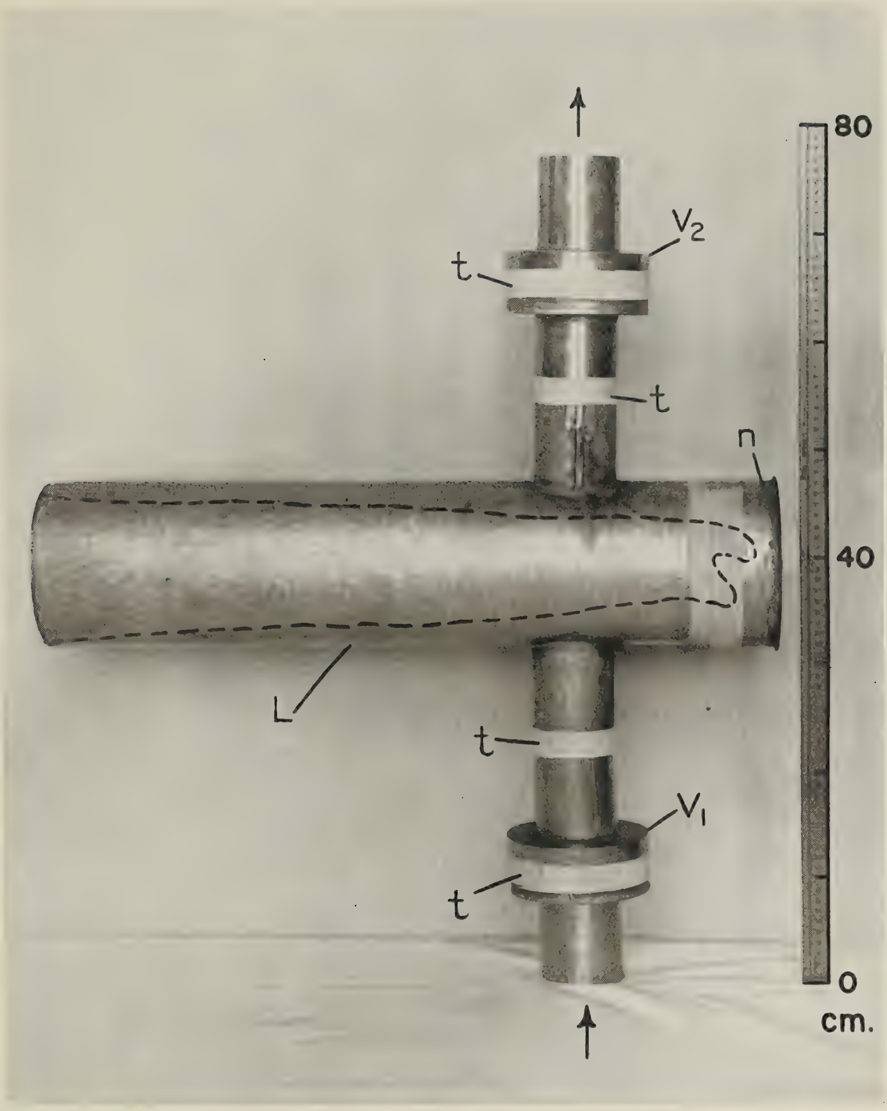


FIG. 4—DIAGRAM OF VALVE IN TRUNK-BREATHING APPLIANCE.

p, aluminum disk; r, r, brass rods with rubber band, h, stretched across them to prevent disk from being driven against opening of upper section of valve; t, adhesive tape making air-tight closure of upper and lower sections of valve. Arrows indicate direction of air current.

A schematic outline of this trunk-breathing appliance with ventilating and metering device is shown in figure 5. The elephant's trunk is in place in the tube L, and the direction of the air current through the valves V_1 and V_2 is indicated by arrows. The air inspired by the elephant was barn air, as-



Trunk-breathing appliance

The tube L, in which elephant's trunk was inserted, was closed by cap n, and connected with inspiratory valve V_1 and expiratory valve V_2. All joinings were made air-tight by adhesive tape, t.

sumed to be the same as outdoor air, for in all these trunk-breathing experiments both doors of the barn (each about 3.5 meters high and 1.5 meters wide) were wide open, and only two or three people were in the barn at the same time. To measure the volume of expired air a spirometer of sufficient size to hold all the air exhaled during 1 minute (not to mention 6 minutes) was out of the question. A 100-liter spirometer of simple construction, S, was, therefore, used as an "expansion chamber." The inner tube of this spirometer was a large "standard 2-inch pipe" (50-mm. internal diameter) which would offer no resistance to the animal's respiratory efforts. The air was withdrawn from this spirometer by the blower system at such a rate as to remove in one minute approximately as much as the animal would exhale in one minute. The spirometer S was directly connected in the line near the valve V_2. The blower system was working continually. With each expiration the spirometer bell rose and with each inspiration it sank. However, as during inspiration air entered through the valve V_1 and the valve V_2 closed off the pipe b (fig. 5) leading to the spirometer, the sinking

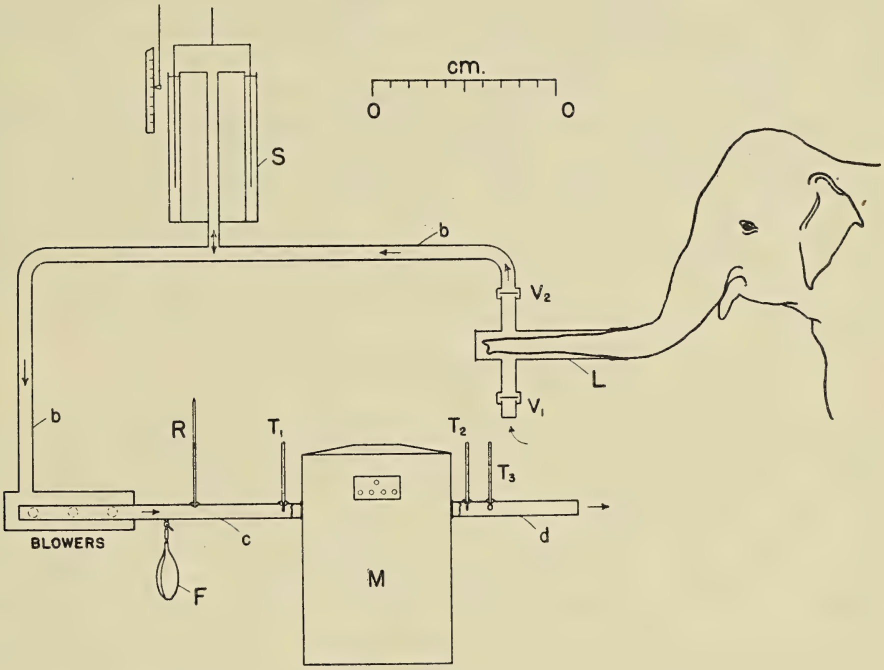


FIG. 5—SCHEMATIC OUTLINE OF TRUNK-BREATHING APPLIANCE WITH VENTILATING, METERING, AND ALIQUOTING SYSTEMS.

L, tube in which elephant's trunk is inserted; V_1 and V_2, inspiratory and expiratory valves; b, b, pipe connecting tube L with blower box; c, pipe connecting blower box with meter M; R, rotamesser; F, Fox bag; T_1 and T_2, dry bulb thermometers; T_3, wet bulb thermometer; d, pipe for discharge of air coming from meter; S, spirometer used as expansion chamber.

of the spirometer bell was due to the continuous withdrawal of air by the blower system. Care was taken to have a slightly positive pressure in the spirometer so that when the spirometer bell was sucked down near the bottom of the spirometer, the inlet valve V_1 would not be lifted and thus increase the apparent total ventilation of the lungs. The pipe c connecting the blowers with the dry gas meter M, the single sampling bag F (by the time the trunk-breathing experiments were made only one Fox bag was employed), the rotamesser R, the thermometers T_1, T_2, and T_3, and the pipe d on the discharge side of the meter, as shown in figure 5, were the same as those shown in figure 2.

Observation of the spirometer bell made it feasible to count the respirations and to have some index of the volume of respiration. Graphic tracing of the respirations was not attempted, because of the magnitude of the respirations, although undoubtedly some simple reduction device for this purpose might easily have been prepared. The elephant experienced no difficulty in breathing, and mechanically the apparatus functioned perfectly. The discussion of the significance of these trunk-breathing experiments, which are to be criticized from the physiological and not from the mechanical standpoint, will be left until later. (See page 235.)

Since the rate of ventilation (about 200 liters per minute) was much less in the trunk-breathing experiments than during the respiration chamber experiments, only one blower was used. Because of the irregular breathing of the elephant, it was possible either for the spirometer bell to be blown out of its water bath or for the bell to strike the bottom end of the outer shell. Hence constant hand regulation of the ventilation was necessary. An observer, therefore, stood beside the butterfly valve connecting with the blower being used and opened and closed this freely, to keep the excursions of the spirometer bell approximately midway of the height of the spirometer. When it was desired to note the volume of any maximum expiration, the entire ventilating system was shut off momentarily by proper turning of the butterfly valve, and the rise in the spirometer for one or two expirations was recorded.

Samples of the air withdrawn from the spirometer were collected not during half-hour periods, as was the case when the respiration chamber was used, but during periods lasting from 7 to 9 minutes. For this reason slight modifications were necessary in the sampling system, which enabled the collection of samples in two ways. A sampling pump was connected with the discharge pipe c (fig. 5), and air from the ventilating air current was drawn into it and expelled twice during the preliminary period of adjustment. Then during the actual period of measurement the piston of the pump was pulled out one-tenth of its length every half minute for 5 minutes. The Fox bag was also employed, with the use, however, of a much larger jet so that the sample (from 1.5 to 2 liters) could be collected in about 8 minutes and not in the usual 30 minutes. For this purpose the disk D (fig. 3) was removed, and the discharge into the Fox bag was regulated solely by the petcock H connecting directly with the pipe c. Because the shortness of the period lessened the chance for diffusion of the gas through the bag and because the carbon-dioxide content of the air in these tests was about 4 per cent instead of 1 per cent, and the gas analyses were carried out only to 0.01 per cent instead of 0.001 per cent, the air-bathing principle was not employed. These two methods, the sampling pump and the Fox bag, gave identical results. Therefore, after the first experiment, in which both methods were used, only the Fox bag was employed.

Although it has been the invariable principle of the Nutrition Laboratory to control the accuracy of functioning of every type of respiration apparatus it uses by carbon-dioxide or alcohol control tests, it was impracticable to make a control test of this trunk-breathing apparatus owing to the field conditions under which the observations were carried out and particularly the time available. Every mechanical principle involved, however, had previously been so thoroughly tested that there can be no criticism of the mechanical construction, notwithstanding the absence of carbon-dioxide or alcohol control tests. Similar types of apparatus used for human subjects at the Nutrition Laboratory have been controlled by Carpenter and Fox[1] by burning various amounts of alcohol.

DISCUSSION OF RESULTS

In the consideration of the various physiological factors studied, no attempt will be made to confine the discussion to any one animal; although the majority of the observations were made on Jap, the conclusions will be based upon the observations on all the elephants that came into our study. Since undivided attention was devoted to Jap for several weeks, it is natural that our judgment should be strongly influenced by the findings on this animal. In general these findings, in so far as they are comparable, are in accord with the observations on the other elephants. But when the data obtained with Jap are not substantiated by the majority of the findings on the other elephants (for example, her apparent immunity to cold—see page 89), this point will be especially stressed.

As previously stated, this monograph has been written not solely for the benefit of the metabolism expert but to meet the demand on all sides for a more general treatment, from a practical standpoint, of the elephant's physiology. It is more than likely, however, that no one practical elephant man will agree with all the statements here included. This can be explained in part by the fact that some of the conclusions are necessarily based upon our experience with the one elephant, Jap. Another explanation is that many elephant men, especially keepers in zoological parks, have had experience with only a relatively few elephants, although they have had many years' experience with these few. Hence it was felt desirable to control the observations on Jap, in so far as possible, not only by observations on other elephants but also by comparison with the statements of men who have had experience with many elephants. It was our good fortune early to establish contacts with Mr. Edward Doherty, who has had 15 years' experience with the elephant herd of the Ringling Brothers, the largest herd of elephants in the Western Hemisphere or, indeed, any place outside of India and Africa. Mr. Doherty's well-tempered speech and caution in statement give authority to his word. Many conferences with him resulted in our securing much information that is believed to be authoritative and worthy of record. The frequent references to him in the pages that follow will show how much his opinions are valued and will indicate our great indebtedness to his courtesy and unfailing interest.

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[1] Carpenter, T. M., and E. L. Fox, Arbeitsphysiologie, 1931, 4, p. 527.

Since this manuscript was written, we have had much correspondence and several personal contacts with Mr. Larry Davis, now (April 1936) in charge of the Ringling herd. Mr. Davis has been most helpful in many ways, in measuring the elephants, in making the tests of the time required for eating bread, and in giving invaluable advice. Our thanks are likewise due to Mr. Walter McClain, in charge of the Barnes herd. In addition, many of the assistants to these gentlemen, most of whose names are unknown to us, rendered every conceivable aid in this complicated study. Without the assistance of all these men the investigation could not have been properly completed, and it can be fairly stated that their efforts made this study possible.

After many years of personal friendship with Dr. Ludwig Zukowsky, Scientific Director of Hagenbeck's Tierpark in Stellingen-Hamburg, Germany, it is more than natural that his mature judgment (based upon contact with innumerable animals) should have great influence with us. As a result, throughout this entire book Dr. Zukowsky's opinions are frequently recorded and form the bases of many statements.

AGE AND LENGTH OF LIFE OF THE ELEPHANT

Reports on the ages of elephants have been exaggerated as much as have statements regarding their heights and weights. Obviously the exact age of an animal can not be known unless the date of birth is known, which is seldom the case, and even when the date of birth is known, a record of the date of death is not always made. Hence many of the statements regarding the age and the length of life of the elephant represent speculations and few can be considered as attested facts. Legend has it that the elephant lives to be extremely old, over 150 or 200 years old. Even so conservative a writer as Sanderson[1] states it is his opinion that the elephant attains to 150 years. In all probability, however, the actual length of life of the elephant is more nearly half this, for in the two authoritative reports by Dover[2] and Richmond[3] the opinion is expressed that seventy years would appear to be a liberal estimate of the potential longevity of the Indian elephant.[4] Of the seventy-eight elephants over twenty years of age in possession of the Madras forest department, Richmond records that only sixteen are over forty years of age, seven over fifty years, and but one over sixty years. Evans states that the extraordinary ages of elephants commonly reported are not true and that an elephant eighty years old has attained the average length of life. The most intelligent elephant men with whom we have talked do not believe that the fantastic statements of the extreme age of the elephant are to be relied upon. They are inclined to think that an elephant eighty years old is a *very old* animal. In general when elephants become very old, their legs do not function well.

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[1] Sanderson, G. P., *Thirteen years among the wild beasts of India*, London, 2d ed., 1879.

[2] Dover, C., Journ. Bombay Nat. Hist. Soc., 1932, 36, p. 244.

[3] Richmond, R. D., Journ. Bombay Nat. Hist. Soc., 1933, 36, p. 494.

[4] For data regarding the longevity of Asiatic elephants who lived for over ten years in the London Zoological Garden, see S. S. Flower, Proc. Zool. Soc. London, 1931, p. 193.

Our interest in the age of Jap was to know whether we were dealing with an animal in the vigor of youth, in the adult stage, or in the decline of old age. Doherty agrees with other elephant men that Jap, at the time of our study, was probably not far from forty years old. Her skin was firm and in good condition, and the folds and wrinkles and general emaciated condition characteristic of older animals were entirely missing in her case. It is highly probable that she was an adult, in other words, that the factor of growth was not present. On the other hand, she was by no means so advanced in age as to be comparable, for example, with the elderly women measured by the Nutrition Laboratory, from whose measurements a concept with regard to basal metabolism has been formulated.[1] That Jap's basal metabolism had begun to decrease as a result of advanced age is highly improbable. A far more probable estimate of her age would be that she was practically in the prime of her physical development. That she compares favorably with the average circus elephant is shown by the lists of estimated ages of the Downie, Ringling, and Barnes herds of elephants. (See table 2, page 22.) If extreme age is attained by the elephant, it is not to be found with the ordinary circus elephant, although individual zoological park elephants may be older.[2] Park animals, however, lead a more serene life than circus animals and do not engage in such strenuous muscular exercise.

The approximate estimated ages of all the elephants upon which observations of one kind or another were made are given in table 2. We believe that all the elephant men gave us their best, most carefully considered judgments of these ages. Probably the closest precise age known is that of No. 4, for Mr. Benson tells us that No. 4 came into his possession at the age of one year. Her age is given, exact, as 11 years. Doherty, in reporting upon ages, with characteristic caution emphasizes that, even with the most expert elephant men, the estimation of age is a matter of judgment, involving statements as to when the elephants were brought to this country, the number of years the owners have been in possession of the various herds, and the physical configuration and condition of the elephants with special emphasis on the condition of their feet and their ears. But even so, the estimates of the ages can not be considered anywhere near so accurate as the estimates of the probable weights. It is reasonably certain, however, that in the Ringling herd there are no elephants of very advanced age, the oldest being given as 60 years and the youngest 20 years. The ages of the elephants in the Downie herd range from 6 to 65 years and those of the Barnes herd from 15 to 40 years.

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[1] Benedict, F. G., New Eng. Journ. Med., 1935, **212**, p. 1111.

[2] The oldest elephant with which we have come in contact is Babe, now in the National Zoological Park at Washington, D. C. Her true age is not known, but she was too old for strenuous circus life and was presented to the park at Washington by the Ringling Brothers.

HABITS

Our discussion of the habits of the female elephant in captivity is based in large part upon a 9-day study of Jap during the daytime only, when many respiration experiments were made, a continuous study of Jap both day and night for nine days, observations during one night on the Ringling herd of thirty-four females, a continuous 8-hour study (10.30 a. m. to 7.10 p. m.) of this same herd by four observers, confirmatory statements from Doherty, in charge of the Ringling herd, and daytime observations on the Al G. Barnes and the Downie herds. Continuous association, night and day, with the Ringling herd in Florida for nearly a week in November gave excellent opportunity for observations on the habits and particularly the physical activity of these animals.

Muscular Activity

Restlessness—The general impression of the elephant is that it is incessantly active. With many elephants that stand for hours at a time shifting the weight back and forth, *i. e.*, "weaving," the activity is as real as it is apparent. With many others it is more apparent than real. Jap was not a "weaver," but she occasionally indulged in these large muscular movements, especially when food was not present. Many elephants, however, are weavers, especially in times of excitement, and hence this external appearance of activity does represent a true and considerable movement of the body. Aside from weaving, however, the muscular activity of the elephant falls into several categories, the movement of the appendages (trunk and tail), of the ears, of the head, and of the main part of the body.

Movement of the appendages—Both trunk and tail are often in continual activity, the tail particularly. Nearer to the tip of the trunk the activity is greater, for the end of the trunk is almost always in motion. Even when the elephant is not feeding, the trunk is raised to the mouth frequently (approximately once a minute) with a wisp of hay or a bit of rubbish. It is also often raised to the top of the head to blow dust or water over the body and is moved all over the different parts of the body. The tail is even more active, and with some animals is in rather vigorous motion. One thinks of tail movements with other animals as associated with the irritation caused by flies. On none of the occasions when these elephants were observed were there what one would term an unusual number of flies. Indeed, flies were conspicuous for the most part by their absence. One would think that with a skin an inch or more thick the elephant would not be troubled by flies. On the other hand, Doherty reports that flies bother his elephants a good deal, and that they tend to gather around the lower part of the legs. The horsefly usually attacks the elephant in the small of the back. Singularly enough, the flies rarely, if ever, get on the ears. Mosquitoes, Doherty thinks, do not affect elephants. In our study of the ear and tail movements particular attention was given to the movements other than those that could possibly be ascribed to the removal of the few flies occasionally appearing.

Ear movements—The ears of the elephant have been the subject of a great deal of discussion because of their size, because they are relatively vascular, and because frequently the highest external temperature of the body is noted on the ears.[1] The ears of the African elephant are enormous, much greater than those of the Indian elephant, and writers on jungle life indicate that they are frequently in motion, especially in hot weather. The smaller ears of the Indian elephant are likewise moved considerably at times. It may be that these elephants in the hot climes of Africa and India move their ears for the purpose of heat regulation. It is difficult to imagine, however, that the hairless animal needs a special heat-regulating mechanism in its ears. The elephant is practically hairless, and yet its ears are considered by most writers as important for heat regulation. If this is true, it is a singular provision of nature. Close study of the ear movements leads us to believe that these represent in large part a nervous reflex, much like the winking of the eyes by humans. With Jap, even in extremely cold weather when there was no appreciable muscular activity and no possibility of heat regulation being called into play, active ear movements were noticeable. Moreover it was increasingly noted by us as our study progressed that the movements of the ears and the tail may legitimately be considered to be reflex indications of psychological *excitement* rather than the functioning of a special heat-regulating mechanism. One wonders that the writers on jungle life, who have seen elephants under conditions of fear and fright, have not considered that their ear movements are indicative of reaction to excitement rather than of heat regulation. For further discussion of this point, with special reference to the greater flow of blood to the ears and the warmer temperature of the ears as a result of nervous excitement see page 158.

Head movements—From the anatomical structure of the elephant's head few major head movements are possible. The elephant can not turn its head sidewise to any great extent, and hence the whole body must be turned in order to see toward the rear. The head movements as such, therefore, are relatively insignificant and infrequent.

Movements of the main part of the body—With the weavers there are obvious, extensive body movements. With a quiet, non-weaver like Jap, the body movements are slow and rarely of any considerable size. There may be a shift of the weight of the body from one foot to another or from one side to the other side, somewhat comparable to the movements of a steer or a cow standing in a stall. The impression is that Jap, so far as the movement of the main body mass is concerned, was actually much quieter than the ordinary cow or steer.

Rôle played by muscular activity in metabolism measurements—For the comparison of the metabolism of one animal with that of another, one is not interested in measuring the 24-hour heat production when the animal is living a normal life, as this type of measurement includes a number of variable factors that could never be standardized for different groups of animals. The daily heat production of Japanese dancing mice, for example, could never be compared with that of a mole on account of the tremendous difference in activity, unless one could measure both animals in complete muscular repose. In any event, the 24-hour energy requirement of a Japanese dancing mouse must, by virtue of its activity, be much greater in proportion to its size than that of the mole. This factor of external muscular activity is perhaps the greatest variant among different animals. The placid, slow-moving Jersey cow, to mention a larger animal, engages in much less muscular activity than the high-strung, mettlesome young horse. Unless animals can be measured in a comparable state of repose, preferably when asleep, variations are likely to be introduced into the metabolism measurements that make comparisons of results on the same animal on different days or of results on different animals unsatisfactory. The first impression one receives from watching an elephant is that it is incessantly active and hence would be a difficult subject for metabolism measurements. This without doubt has retarded active steps to measure the metabolism of the elephant. More intimate studies of the animals at the zoological parks and particularly in various traveling shows indicated that, although the elephant seems to be incessantly active, this is notably the case with elephants that are weavers, and there are but few elephants that are not weavers. Close watch of these occasional non-weavers showed that the impression of apparently incessant muscular activity was incorrect and that, although there are physical movements, they are almost invariably inversely proportional to the weight of the part moved, decreasing in magnitude from the large movements of the last decimeters of the trunk and the tail to the smaller movements of the main body mass. The lower end of the trunk, for example, which is almost never at rest, and the tail represent but insignificant percentages of the total weight of the animal. The largest part of the body, the main body mass, is moved very slightly and slowly by elephants that are non-weavers. Hence in the case of a non-weaver, the extraneous muscular activity is small and is confined almost exclusively to the lower third of the trunk, the tail, the ears, the minor lateral movements of the head which take place with varying degrees of frequency, and only insignificant movements of the major parts of the body. Consequently one great objection to the use of the elephant in gaseous metabolism studies, namely, its seemingly constant muscular activity, in large part disappears. Jap, as already stated, was a non-weaver. Inside the respiration chamber her movements were essentially the same as those when she was chained in the barn, that is, the end of the trunk was continually moving, the tail, also the ears moved occasionally, the head rarely, and the entire body only slowly and infrequently. In no way perhaps than from this analysis of motion could the danger of false interpretation of an ocular impression of activity be more strikingly shown. Graphic records of the activity of an animal of this size by the ordinary pneumograph method were not impossible, but impracticable because of the emergency nature of the study. Several skilled observers, however, were of the opinion that the major body movements of Jap were insignificant. Of the animals whose metabolism has been measured in respiration chamber experiments by the Nutrition Laboratory and whose stall activity has been carefully studied over a number of years, the nearest to the elephant in size are the cow and the steer. It is believed that the activity of Jap while inside the respiration chamber was proportionately far less than that of the average cow or steer, not excepting the minimum activity of these ruminants during prolonged fasting.

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[1] Benedict, F. G., Fox, E. L., and M. L. Baker, Amer. Journ. Physiol., 1921, 56, p. 464; *idem*, Proc. Nat. Acad. Sci., 1921, 7, p. 154.

Influence of absence of food upon body activity—One of the prerequisites for basal metabolism measurements is that the animal should be in the "post-absorptive" condition. This, with humans, is commonly assumed to occur 12 to 14 hours after the last meal, with dogs 12 hours after food, and with ruminants a much longer time, two or three days perhaps, because of the large capacity of the paunch for reserves of food. In the early plans made for studying Jap it was hoped to make some respiration experiments with her in the post-absorptive condition, but conference with her keepers indicated that she would resent greatly withdrawal of food. (See page 233.) The wild elephant munches food a good part of the twenty-four hours. Food is apparently indispensable to the body comfort of the elephant, perhaps more so than with any other species of animal the Nutrition Laboratory has studied. As Herbert[1] has expressed it, the "elephant's life is one continuous meal." As long as any food is before it, the elephant will pick up small particles, even when the appetite apparently is fully satisfied. The trunk is in incessant motion, turning over the hay, picking up a wisp or two here and there, and carrying it to the mouth. Circus elephants are fed five or more times a day. Rarely is hay not within reach of any of the animals, and even after they have eaten their larger portion, they continue to reach, search, and nibble on bits of hay. The only time when the elephant is not eating during the twenty-four hours when hay is available is when the animal is lying down, but since the period of lying is relatively short, it is eating almost constantly. The Barnes herd of elephants, which engaged in extreme muscular work, were noted lying more frequently than is customary with elephants during the day, but even when lying these particular animals, before going to sleep, almost always were stretching for bits of hay to eat. This habit of eating constantly can hardly be sufficiently emphasized when one considers the difficulty of trying to make gaseous metabolism measurements to approximate the basal metabolism measurements so common on other animals. There is no period of the day when the elephant is in the post-absorptive state. This animal is so dependent upon the passage of food through the intestinal tract that it is irritable and restless without food. This feeding habit defeated our hopes of obtaining basal metabolism measurements in the strict sense with this animal. (See page 234.)

Muscular activity during the eating of food—When food is present, the activities of the trunk and the jaws perceptibly increase. The trunk is continually in motion, lifting portions of food to the mouth approximately once every thirty seconds. The motion of the jaws is mostly up and down, with some forward and back motions but no sidewise motion. The actual muscular work of chewing can not be great, since the hay eaten is poorly comminuted, as demonstrated by the feces which are comprised chiefly of pieces of apparently unaltered, chopped hay averaging about 2.5 cm. in length, and sometimes 15 to 20 cm.

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[1] Herbert, A., *The Elephant*, New York, 1917, p. 206.

Body Position

The elephant almost invariably remains standing. It is made to lie down frequently in circus performances, but normally it apparently lies down for only a relatively short time during the night and almost never during the day, except when unusually tired following severe work or because deprived of sleep or the privilege of lying down (as is frequently the case when elephants are on tour and have no rest). On Sunday, when on tour and not traveling, elephants often lie down during the day. Other than that the ordinary time for lying down is during the last half of the night. On the Sunday when the Ringling Show was in Bangor several elephants were noted lying down in the latter part of the afternoon. But the most striking illustration of day sleeping was with the Barnes herd of eighteen elephants, ten of which were found to be lying down at about 5 o'clock in the afternoon and most of these sound asleep. These particular elephants had been working intensely during the morning at their tasks of drawing the vans to the circus lot, raising the poles and canvas, and pushing the various animal vans into place. Probably this group does the hardest work of any elephants, certainly any connected with circuses.

The process of lying down is a massive one, as is to be expected with such a huge animal, and is comparable to the movements of the horse in getting up and down. There is usually a settling of the entire body onto the hind legs, the fore legs are spread out, the animal lies on its belly, and then rolls onto its side. The reverse process is employed in standing up. The elephant gets up from its lying position with the fore legs first. as does the horse.

Sleep

It is the current belief that the elephant rarely sleeps and, if so, for only a short time. Evans states that the elephant's sleeping is confined to a few hours, usually from 11 p.m. to 3 a.m. Our observations on Jap, the Ringling herd, and especially the Barnes herd (see page 72) lead to the conclusion that elephants not uncommonly go to sleep, that they can get sufficient sleep standing up and, given the opportunity, will sleep lying down and prefer to do so. As Zukowsky has pointed out, however, it is difficult to make observations on sleeping elephants, as their slumber is very light and they spring up, alert, at the least disturbance. For this reason, our rather extended observations on the sleeping elephant are here recorded.

SLEEP STUDY WITH THE ELEPHANT JAP

Our particular interest was in the sleeping habits of Jap, as we hoped to make some metabolism measurements on her while she was asleep. She did not sleep inside the respiration chamber, however, save dozing for a few moments on one day and then in the standing position. In the first series of observations on Jap no measurements were made after 8 p.m. or before 9 a.m., and she never went to sleep lying down during this study. On one occasion the keeper reported that she had been asleep for a few minutes while standing inside the respiration chamber, assuming the characteristic pose of quiet, with the trunk hanging down, the tip of the trunk resting slightly curled up, on the floor, with eyes closed, and with no visible body movements. With the Ringling herd this position, a sort of "cat nap," is never held for more than a few minutes.

In the second series of measurements on Jap, special observations regarding her sleeping habits were made continuously for twenty-four hours each day for nine consecutive days. On the first night, April 2 to 3, the animal did not lie down at all, perhaps because of the novelty of having the observers stationed in the barn to collect feces and urine and because of the illumination from an electric light. At 3.40 a.m., however, she apparently took a short nap while still standing. At this time the temperature of the barn was about 16° C., perhaps the highest temperature recorded throughout the nine days. On the next night, April 3–4, she lay down at 12.30 a.m. and went to sleep immediately. At 1.55 a.m. (environmental temperature 8° C.) the elephant was reported as "snoring." She awoke and stood up at 2.20 a.m. and lay down again and went to sleep immediately at 3.58 a.m. At first, for several minutes, she switched her tail on the canvas (kept under the rear part of her body to aid in collecting feces uncontaminated by the débris on the barn floor) but later stopped and began her heavy breathing. She inhaled and held her breath for about five or six seconds and exhaled in five seconds or a little longer. At 6 a.m. she stood up.

At midnight on April 4–5 Jap was extremely restless, for the hay had all been eaten. At 2 a.m. she was so active that hay had to be given to her. She lay down at 3.18 a.m. (barn temperature 8.9° C.) on her left side and slept, snoring heavily with deep, regular respirations. At 5.15 a.m. she was still asleep. At 6 a.m. she stood up. On April 5–6 at 11.30 p.m. she slept standing up, with but about three respirations per minute. At 1.25 a.m. she was very sleepy, dozing off at times, but would not lie down. At 2.10 a.m. she was wide awake and eating and showed no inclination to lie down. At this time the barn temperature was 9.7° C., the outdoor temperature was 2.8° C., it was snowing, and much colder than it had been. At 4 a.m. Jap lay down, but without any hay for a pillow. (See page 71.) At 4.30 a.m. she was snoring heavily but woke suddenly at 5.46 a.m.

On April 6–7 she lay down at 1.39 a.m. and went to sleep. She woke at 2.26 a.m., but went to sleep again immediately after stretching and shifting her trunk. At 3.10 a.m. she stood up. At 4.23 a.m. she was sleeping while standing. On the afternoon of April 7 she dozed with her eyes closed, breathed heavily, with the trunk hanging limp and resting on hay. This lasted only fifteen minutes. On April 7–8 at 1.20 a.m. she lay down and snored heavily. At 3.03 a.m. she stood up quickly and began eating. On April 9 at about 2 a.m. she showed no indications of lying down, as she was asleep standing up. It was very windy and cold outdoors. At

3.18 a.m. she lay down. At 4.55 a.m. she stood up. At 5.10 a.m. she slept, standing, for a short time.

On April 9–10 at 1.30 a.m. Jap tried to break loose. All her hay was gone, and she trumpeted continually. Hay was fed to her at 2.05 a.m., and she lay down at 3.10 a.m. (barn temperature 9.8° C.). At 4.43 a.m. she stood up, but at 4.58 a.m. she lay down again. At 6.30 a.m. she was still asleep. At about 7 a.m. she stood up (barn temperature 6.8° C.). On the last night of the series, April 10–11, she lay down at 2.34 a.m. and stood up at 4.05 a.m. She lay down again at 4.30 a.m. and stood up at 6.08 a.m.

In table 3 are summarized the times when Jap was lying down and probably asleep, on the nine consecutive nights between April 2 and April 11, 1935. Although Jap, as most elephants, slept but a few hours each night, characteristic features of her sleep attracted our attention. The hours for sleep were by no means regular. Jap was apparently very sensitive to her environment. Light and noise of an unusual character seemed to retard her tendency to sleep. In sleeping, she always lay on the left side. There are two possible explanations for this other than instinct. One is that when she was lying on her left side, her back was toward the side of the barn and she could see everything in the rest of the barn, including the operators. Furthermore, because of the way she was chained, it was easier for her to lie on the left than on the right side. The characteristic position of the trunk of Jap when asleep was coiled up like a snake, with the end on top to make it easy to breathe. The only movements made by Jap when asleep were to stretch somewhat and to discharge gas and feces per rectum. She fell asleep as soon as she lay down.

TABLE 3—*Time spent by Jap lying down and presumably asleep on nine consecutive nights*

Date	Time	Hours
1935		
April 2–3	....	0
April 3–4	12.30 to 2.20 a.m.	3¾
" "	3.58 6.00 a.m.	
April 4–5	3.18 6.00 a.m.	2¾
April 5–6	4.00 5.46 a.m.	1¾
April 6–7	1.39 3.10 a.m.	1½
April 7–8	1.20 3.03 a.m.	1¾
April 8–9	3.18 4.55 a.m.	1½
April 9–10	3.10 4.43 a.m.	3½
" "	4.58 7.00 a.m.	
April 10–11	2.34 4.05 a.m.	3¼
" "	4.30 6.08 a.m.	
Average hours lying asleep nightly on nine nights		2¼

SLEEP STUDIES WITH THE RINGLING AND BARNES HERDS

Since the observations on any one animal, not only with regard to sleep but other factors, may be thought not to be necessarily characteristic of that species of animal, the more general observations on the sleeping habits of the Ringling and the Barnes herds are of special interest. The Ringling elephants are not living under abnormal conditions for them. Many of them have been with the herd for two or three decades. They are all well looked after, are all in good health, and contented, and rarely have any disease. Apparently the elephant quickly adjusts itself to a new situation, such as a change in environmental temperature and in food; for example, the substitution of dry baled hay for tropical, succulent shoots. Hence one can assume that they become easily adjusted to all other factors. The sleeping habits of a herd, therefore, can not be far from normal. Since the Ringling herd is one of the largest elephant herds, a special study of their sleeping habits seemed worth while. These elephants, thirty-four females, are chained fairly closely together when on tour. Under ordinary conditions, therefore, it would be impossible for all of them to lie down at once. When traveling on tour, they are transported in three railroad cars, packed in tightly so that they can adjust themselves to the motion of the train better than they could if standing isolated. Occasionally one or two animals may lie down during the transportation, but for the most part they have to remain standing until they arrive at the next city. If they sleep, therefore, while on the train, they must sleep standing. Doherty emphasized that many elephants sleep standing. Indeed, as we were talking with him at midnight in the circus quarters on one occasion during a week's stay of the Ringling herd in Boston, we could see many elephants with their eyes closed and their trunks hanging loosely, with the ends curled up a bit and resting *quietly* on the floor or, if the next elephant was lying down, with the trunk laid on the next animal's side.

At night when they are not traveling on the railroad and space permits, as at the Boston Garden, a few of the larger elephants are taken out of the line and given more room in which to lie down. This also gives more room for their near neighbors in the place from which they were removed. These elephants are fed after the evening performance (about 11 p.m.) and go through the usual amount of motion, playing, and often blowing the hay over their backs. There is little noise among the elephants when at rest, just the sound made by wisping the hay about, now and then a low rumble, and rarely a squeak. Under these conditions the elephants seem contented and placid, and it is difficult to imagine them as being excitable and liable to stampede. Yet under precisely these conditions they are constantly watched by two trained watchmen. When the appetites of the Ringling herd are satisfied, the elephants may then exhibit a peculiar act in what at first sight seems almost a "nesting instinct." Any refuse or good, uneaten hay is carefully scraped together and made into a nest or, more properly speaking, a pillow. This pillow is placed not under the head but under the body. As the elephant rolls over flat on its side, the hay takes the shock but (as we observed when the Ringling elephants were in the large exposition building in Boston, which had a cement floor) the head, when it went down, struck the floor with a resounding thump. This making a pillow of hay is done because the animal finds the cement floor cold. When the elephant lies down on a wooden floor, such a pillow is not prepared. Thus at Sarasota with a plank floor no hint at hay protection was seen, though frequently the planks were missing and the floor was very uneven.

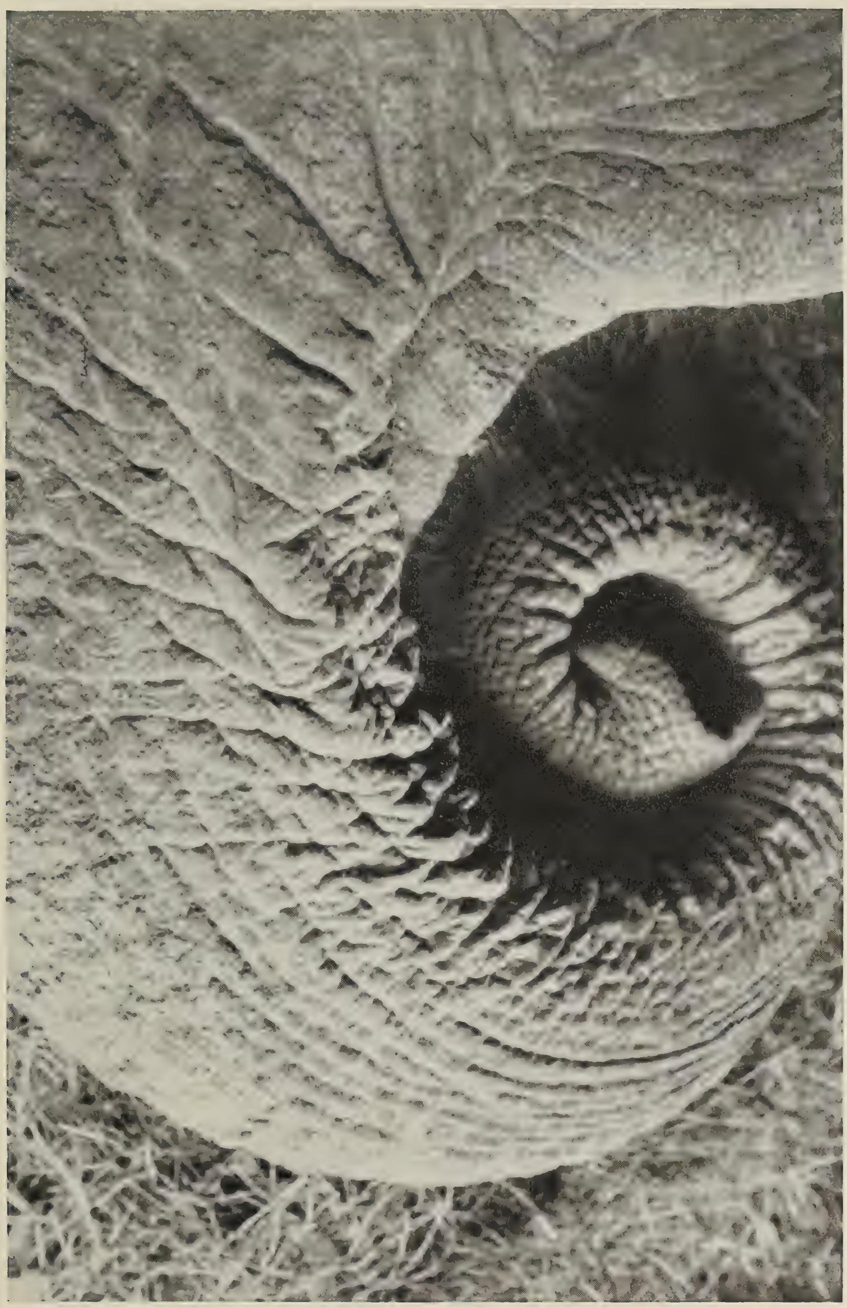
Even when some of the larger elephants are taken out of line, there is not room enough for all to lie down at once. Hence the first to lie down has the advantage. The elephants never seem to learn this and show not the slightest desire to be the first one down. They munch and play for a certain length of time and then only are they ready to make their pillows. If, however, one elephant has been lying down for some time and its neighbor becomes tired, the neighbor begins annoying the other elephant, hitting it with her foot and trunk until this elephant stands up and the tired one can lie down.

Doherty emphasized that elephants prefer to sleep where it is quiet. Yet it was very noisy at the time of our Boston observations. The men were quiet, although now and then a few words were spoken in a loud (not shouting) voice to those of the elephants inclined to get into mischief. But lions were roaring, the sea lions barked incessantly, and the elephants that could not lie down were moving around, hitting the sides of those who were lying. One could not call the conditions reposeful. Yet the elephants went to sleep or at least dozed without difficulty.

With the Ringling herd in the tent at Bangor, Maine, it was noted that several animals lay down to sleep in the late afternoon (Sunday). With the Barnes herd, the working herd of elephants, the standing sleeping position was frequently assumed during the daytime and (precisely as was noted with the Ringling herd on the nights spent with them) they seemed to drop off into a deep sleep, with deep inspirations, within a minute or two after lying down. Indeed, on the day we were with them at St. Stephen, New Brunswick, ten out of the eighteen animals in the Barnes herd were found lying asleep at about 5 p.m. The body position of these elephants while lying was carefully studied, and a photograph was taken of the characteristic position of the trunk (see Plate 8) which is coiled up, probably instinctively for protection. The end of the trunk is not free, as one would expect, but is partly closed by the coil itself. It was found that occasionally Jap slept with the tip end of the trunk somewhat elevated, so as to provide a freer access to air.

OBSERVATIONS ON THE RINGLING HERD IN FLORIDA

In Florida there was considerable activity going on throughout the day. The elephants were fed frequently. There was no circus excitement and no undue disturbance of the regular hours of sleep, as the elephants had always a good night's rest. The result was that there was rarely an indication of the animals' sleeping or dozing during the daytime or, indeed, well into the evening. The entire evening until midnight on one night and from midnight to 8 a.m. on another night was devoted to a study of their sleeping habits, with special emphasis on when they lay down, whether they were sleeping, and likewise whether they were inclined to lie more on one side than on the other. A survey of the entire herd showed that at 12.30 a.m.



CHARACTERISTIC POSITION OF TRUNK OF ELEPHANT, WHILE LYING ASLEEP.

This photograph was taken of one of the Al G. Barnes herd, while on exhibition at St. Stephen, New Brunswick, August 1, 1935.

twenty-three elephants were lying down, most of them on the left side. At 2 a.m. twenty-four were lying down, mostly on the right side. At 3 a.m. twenty-eight were lying, approximately half on the left and half on the right side. At 4 a.m. twenty-one were lying, about equally divided as to the side upon which they rested. At 5 a.m. twenty-two were lying and at 5.30 a.m. but fifteen were lying, at both times about an equal number on the right and left sides, respectively. At 6 a.m. but one was lying, and on the right side. Two elephants (Nos. 18 and 40) always lay on the right side, and three (Nos. 16, 36, and 41) always on the left. Although there were only three observations on No. 24 while lying, she was in all instances (at 3.00 a.m., 5.00 a.m., and 5.30 a.m.) on the left side. The other elephants lay at will either on the right or the left side and changed their position not infrequently.

The elephants were up and down throughout the entire night. Almost invariably when they stood up, it was to urinate or defecate. They did not lie down immediately thereafter, however, and we have no record as to the actual total amount of time spent lying. The elephants rarely lay down before midnight, only four having been observed during our stay at Sarasota to lie earlier than this. At one time (about 2.00 a.m.) thirty of the thirty-four elephants were counted as lying down.

A tremendous amount of energy is apparently expended by these large animals in getting up and lying down. It seemed a much greater effort for the elephants to get up than to lie down. This was particularly the case with Alice at the New York Zoological Park, who, perhaps by virtue of her age, found difficulty in getting up, rolling about considerably until impetus was obtained to bring the body into an upright position. A survey of the Ringling elephants showed a similar, although not so marked, effort. It is clear that the mere effort of standing up and lying down is a considerable one. For that reason no observations on the heart rate were made immediately following the change in body position, either from the standing to the lying position or *vice versa.*

It is a curious fact that when elephants are fastened to their stakes in the barn, they lie readily on either side, but in their act in the ring they are trained to lie on one side, and it would be difficult to induce them to lie on the other side. They would have to be trained specially for this purpose.

The general conclusion from all these observations is that usually the elephant sleeps immediately upon lying down. At times, however, after all the hay has been eaten, the elephant may actually doze in the standing position, in which case the characteristic position is standing with the head and the trunk motionless, the end of the trunk resting quietly on the ground. This position is not maintained long, rarely over fifteen minutes at a time, but was frequently observed with Jap and was noted with the Ringling herd. In the wild, the elephant is stated to be more of a nocturnal animal, but captivity has reversed its habits. It is fed by man during the day and is called upon for performance during the day. Hence what sleeping is done occurs usually between 1 a.m. and 6 a.m., although occasionally dozing or indeed, sleeping in the lying position occurs also during the daytime.

Business or Professional Activities of the Elephant Jap

During the active business season Jap's chief occupation is working with a circus, on tour from approximately the middle of April to the middle of November. At such times she not only is called upon as a show animal but, owing to her massive size and equable disposition, she does a great deal of work around the lot, moving vans in place, hauling them out of the mud, and pulling all the tent stakes after the performance is over. A hint of the amount of energy expended in this work is obtained from the statements of the keepers that on tour Jap is fed three times as much as when in permanent quarters, so far as hay is concerned, and has a liberal supplement of bran mash, oats, and the like. In the winter, after the circus season is over, she is occupied intermittently in various processions, political and otherwise, and in theatrical engagements. In the late fall and early winter of 1934-35 she was used for advertising in the streets of New York, wearing various advertising banners on her sides. From Campgaw to New York (30 miles) she was transported in an open truck, frequently making the trip and return in one day. In the theatre and on the street obviously her activity consisted merely in walking about at a moderate pace, accompanied by her keeper. At the time of the respiration experiments she was in the barn, chained the entire time. Rarely did she walk twenty-five or thirty yards from the barn to the watering trough. Occasionally she walked 150 yards or more to a tree in the field, to which she was chained during some special work in the barn, especially during the time the respiration chamber was being constructed.

TEMPERAMENT

So much of legend attaches to nearly every elephant in the show business that it is difficult to unravel the truth from the large mass of fiction. Legend has it that Jap had, in circus parlance, become a "bad animal." She was unruly and would not cooperate with the other animals, and it became too much of an effort to handle her. She had been with the Barnum show for twelve years when, owing to her incompatibility, she was sold. Meanwhile she had killed a man. Apparently the difficulty was with her association with other elephants, for almost immediately following her isolation she became an entirely different animal. She prefers to be alone, will not work with other elephants, and when alone is most docile and tractable. So far as we were concerned, she presented no disciplinary problem. The writer was alone with her for an hour and a half every noon for ten days, studying her body activities, and saw nothing to suggest irritation and viciousness. She was possessed of great inquisitiveness and incessant playfulness amounting to mischief, having a tendency to destroy everything within reach, breaking a chair, a ladder, or even smashing pieces of lumber as large as 5 by 10 cm. On several occasions she has knocked boards off the side of the barn, and yet on these occasions she stopped instantly when a word of caution was spoken. Possibly one cause of her trouble with her keepers was that they had been changed several times and many of them did not know her particular cues, became irritated at her apparent lack of cooperation, and gave her punishment. After two weeks' work with her, the writer personally can not feel that any one could wish for a more tractable, docile beast. This observation was important in connection with the respiration experiments, for measurements on a highly excitable, nervous, irritable and vicious animal would have given results in no way comparable to those made with most animals in metabolism studies. Supplementary observations on the Ringling herd suggested likewise that for the most part elephants are extraordinarily intelligent, tractable, docile, quick to obey, and present no great disciplinary problem.

Excitability and Tendency to Stampede

The apparent immunity of Jap to sudden excitement, the result perhaps of her unusual experiences with street noises, elevated trains, and fire engines, indicated that she would be particularly placid in our metabolism study. In one particular, however, she showed great excitability and distrust of what was going on. Since she was chained both by a front and a hind leg, it was impossible for her to turn her entire body quickly to see what was going on behind her. The result was she had a tendency to become restless when any unusual action was going on outside of her field of vision, that is, toward the rear. In general she did not like to have anything going on that she could not see. Whatever she could actually see in front of her did not frighten her, but sudden movements behind her that she could not see troubled her. When she was put in the respiration chamber, it was necessary to put on the massive door (3 by 3 meters) behind her. When this door was brought up directly from the rear, it disturbed Jap greatly. Finally it was suggested by her keeper that the door be brought up to one side and slid into position like the door of a freight car. It took part of a day to accustom Jap to the closing of this door, and at no time was she entirely free from apprehension as the door was closed, although toward the end of the experimental series she gave this procedure relatively little attention. When she was inside the respiration chamber any sudden body movement might have demolished the walls, but her apprehension never became so great that she made a sudden jump, although we always feared it.

With the Ringling herd, when at Bangor, there were two instances showing a flighty disposition of this nature. On one occasion a horse broke loose and ran behind the elephant tent. The back flap of the tent was down, the elephants could not see out, and yet they heard the commotion. Suddenly five elephants turned in an instant, making a turn of the body of over 180° simultaneously and in the fraction of a second. Having seen that there was no particular danger at hand, they turned back slowly and became quiet, but their first movements had been startlingly rapid. On another occasion one troop of five elephants was taken into the main tent for rehearsal in the afternoon, but the second troop, which usually followed it immediately into the ring (led by elephant No. 17), was not taken out. No. 17, who stood next to the last animal of the other troop that had gone out, was tremendously excited and upset by the fact that something unusual had taken place. Her agitation was extreme. She trumpeted, uttered shrill cries, and continually turned her body around, until it was necessary for the keeper to stand beside her with a hook to keep her within bounds. Her excitement was not transmitted to the others, although it was feared that she would agitate the other elephants in her troop and more especially the five elephants rehearsing in the main tent, thereby not only spoiling the act but endangering the life of the trainer during the performance.

This tendency for stampeding or flightiness is apparently so general, at least with elephants in captivity, that several keepers are constantly on guard with circus elephants. Even in the case of Jap, who was quiet and isolated from other animals, it was necessary to have a man in attendance all the time. In fact, the keeper slept in the barn on a cot. With the Ringling herd on tour, two keepers are on continuous watch all night, directly in front of the elephants so that they can see the entire line of thirty-four. Generally no trouble is expected, but as Doherty commented, if a zebra broke loose and came running into the elephant section, the elephants would become so startled that they might pull away their stakes and cause much damage. Indeed, the presence of any *strange* animal, no matter how small, is apt to cause disturbance. A strange dog barking, or any other small animal, usually will excite one of the members of the herd, and she in turn tends to excite all the others.

Although stampede did not take place, the preparations made to prevent a possible stampede by the Barnes herd at St. Stephen illustrated the extreme caution needed by elephant trainers. Shortly before the afternoon performance a heavy electrical storm came up, with lightning and thunder. By order of McClain, the head elephant man, the elephants were unshackled and massed together, side by side in solid formation, with a man at the head of each animal with his hook. At each end of the line was a non-temperamental elephant which, experience had shown, was not apt to stampede. If any flighty animal started to stampede, its space for action was limited and the docility of the others, as a whole, would hold it in check. Although the head keepers and the individual keepers were obviously anxious and feared a possible stampede, on this particular occasion the animals were apparently unaffected by the crash of the thunder and by the lightning and ate their hay with the greatest placidity.

In this study considerable information was obtained with regard to the relationship between the elephant and the activities of smaller mammals, dogs, rats, and mice. No one legend with regard to the elephant has persisted any more than its supposed terror at the sight of or contact with a mouse. This point has been discussed with every elephant keeper with whom we have been associated. Based upon these discussions and also upon our own personal observations, the following comments are made. Practically no elephants now are without continuous experience with rats and frequently mice. The very nature of the elephant's feed (hay or grain) attracts these rodents. Hence they are by no means strange. They are usually about at night, but on several occasions in the daytime we have actually seen rats and mice eating grain within a few feet of the elephants, and apparently with complete indifference on the part of both animals. In the elephants' winter quarters there are frequently large numbers of rats running around the elephants, particularly at night, as noted by the night watchman. If the rats come in contact with the elephant and run over its trunk or its leg, the elephant will be startled and will often stand up and begin to trumpet. This, in turn, will start many of the other elephants trumpeting, although the others will have no means of knowing what the cause of the disturbance is. On the other hand, we have placed a mouse directly on the trunk of an elephant, who was utterly indifferent to it.

The facts are that the elephant is startled by *any* unusual sound or noise. A rat or a mouse running over a piece of paper would startle it. There is no reason to believe that the rat or particularly the mouse is any more specifically startling to the elephant than is any other animal making a sudden or unexpected movement. The old concept that the elephant is afraid of the mouse because the mouse can crawl into its trunk is absurd on the face of it, for the mouse could not enter the trunk but a few centimeters before a terrific expiratory blast would dislodge it with sufficient force probably to kill it. It is a fact that elephants will kill these rodents by stepping on them, if they can.

The instability or flightiness of elephants is the characteristic that made them so unreliable and dangerous to their own troops during their early use in warfare. Historians cite frequently that the elephants, by stampeding, did more damage to the men of their own army than they did to the enemy.

BREEDING HABITS

The sex life and the reproductive activity of the elephant might, at first thought, have no place in this memoir. But in view of Riddle's observations that ovulation in birds affects the metabolism [1] and in view of the conclusion that in metabolism measurements on women the menstrual cycle must be taken into consideration,[2] information was desired regarding the œstrus cycle in the elephant, with particular reference to Jap. The Nutrition Laboratory has made no direct observations on this factor but, on the other hand, it has made inquiries into the subject more thoroughly than perhaps has thus far been done and probably with a more critically scientific objective. The previous literature on the œstrus cycle of the elephant has been consulted. Innumerable conversations have been had with various elephant keepers, and an especially illuminating correspondence on the matter has been had with Dr. Zukowsky of the Hagenbeck Tierpark in Hamburg, Germany. The sex life of the elephant, like so many other phases of its life, is surrounded by so many fantastic legends that it is difficult to distinguish between what is true and what is false. Careful weighing and assorting of the information obtained has been made, and the results of this special study are here reported, not as facts attested by Nutrition Laboratory experience but as highly probable statements of the true situation.

Age of reaching sexual maturity—The elephant becomes sexually mature probably somewhat younger than has been commonly thought. The exaggerated statements that attribute extreme length of life to the elephant have, to a certain extent, been reflected in the belief that maturity is attained fairly late. There seems to be good evidence that both male and female can become sexually mature and produce young at not far from ten years of age. There are the specific instances of Ellen at the Copenhagen Zoological Park who was 13 years of age at the time of the birth of her first baby,[1] Cora at Munich who was reported to be 9 years old when her baby was born, and Boy (sire of the baby born at Munich) who was stated to be but 10 years old.[2] Lorenz Hagenbeck[3] has reported an instance of a bull that was sexually mature at the age of 11 years, and Major Flower[4] has recorded several instances of elephants giving birth to young at ages ranging from 11 to 14 years.

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[1] Riddle, O., Proc. Amer. Philos. Soc., 1927, **66**, p. 497; *idem*, Journ. Amer. Med. Assoc., 1929, **92**, p. 943; Riddle, O., and P. F. Braucher, Amer. Journ. Physiol., 1934, **107**, p. 343.

[2] Benedict, F. G., and M. D. Finn, Amer. Journ. Physiol., 1928, **86**, p. 59.

Mode of mating—The œstrus cycle, the sex play, and the mode of mating are treated in detail, with extensive photographs and literature references, by Schneider.[5] The general statement may be made that the congress differs in no way from that of normal domestic animals.

Discharge from temporal glands—No one factor in the study of the sex life of the elephant has caused any greater difference of opinion and more pronounced opinions perhaps than the supposed correlation between the activity of the temporal glands and the intensity of rut. Both the male and the female have these glands. The fact that there is a discharge from them at irregular intervals is by no means definitely associated with the period of heat.[6] On the other hand, in those relatively few animals in which rut is pronounced there seems to be a correlation between the intensity of the temporal gland discharge and the intensity of rut.[7] In the case of the Ringling herd these vents flow about twice a year, but only with twenty of the thirty-four elephants. The impression is that this phenomenon occurs only with those elephants 25 years old or over. The vents on a male formerly with the Ringling herd did not run until he was 30 years of age or older. In our own personal experience with sixty-three elephants (62 females) and repeated contacts with the thirty-four females of the Ringling herd in May, July, and again in November, we saw at no time an elephant whose temporal vents were flowing, so that if this be taken as an index of rut, no signs of rut, based upon this phenomenon, were observed. All vents were kept open by being cleaned by the keeper and well lubricated with vaseline. The intelligent keeper (Ryan) who had charge of "Big Rosie," a splendid elephant used in a large spectacle in New York City at the time of writing (December 1935), assured the writer that at no time during the three years he had had charge of her did these vents flow. This large elephant, although mature, is by no means old.

Cheek vent—Although probably in no wise associated with the temporal glands, there is another small vent or opening on each cheek of the elephant, located almost vertically below the temporal vent and at a distance about halfway between the eye and the mouth. Our attention was called to this vent by Keeper Clark, at Franklin Park in Boston. This vent was found on the two Franklin Park elephants, likewise on Babe, an elderly female in the collection of Dr. W. M. Mann, at the National Zoological Park in Washington, D. C., and on "Big Rosie" in New York. The vent is characterized by having a cluster of small hairs around the opening. No anatomical record indicating their significance has been found.

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[1] Schiött, J., Zool. Beobachter (Zool. Garten), 1908, **49**, p. 133; Hvass, H., Zool. Garten, 1932, **5**, p. 191.

[2] Antonius, O., Zool. Garten, 1932, **5**, p. 170.

[3] Grimpe, G., Zool. Garten, 1933, **6**, p. 197.

[4] Flower, S. S., Proc. Zool. Soc. London, 1931, p. 191.

[5] Schneider, K. M., Zool. Garten, 1930, **3**, p. 305.

[6] As early as 1799 there is a notation by J. Corse (Philos. Trans. Roy. Soc. London, 1799, Pt. 1, p. 31) that he could not confirm an association between the temporal gland swelling and the appearance of rut.

[7] Schiött (Zool. Beobachter, 1908, **49**, p. 133) emphasizes the notable flow of the temporal glands of a large male, Chang, at Copenhagen, who appeared to be rutting twice each year.

Sex activity—The sexual activity of the female, at least, is at a very low level, with only rarely appearances of excitability at all comparable to the excitability noted with most domestic and other large animals. Evans[1] has never observed any apparent signs of heat in the female. He states that his friends who "had seen a great many elephants and had been amongst elephants for many years, had not seen anything noticeable among female elephants" beyond the fact that "the female when in that state utters certain peculiar sounds." Steel[2] believes that the deficiency of sexual instinct among domesticated elephants is probably due to underfeeding.

So far as is known, Jap has never been bred, and certainly during our experience with her she gave no external evidence of sexual excitement such as unusual irritability, muscularly or nervously. The only act possibly attributable to a sex impulse was her tendency to produce pressure on the nipples with the end of the trunk. Her trunk, in somewhat of a rhythmic motion, played first around the padlock on the right front foot, then rose to one of the breasts, and then was pulled down. The trunk was at the breast rarely more than a few seconds, and this occurred only periodically and by no means throughout the day. The external genitalia did not appear abnormal or unusual, and the only evidence of sexual excitement was this tendency to aspirate the nipples. Discussion with the attendants of Jap brought no satisfactory information on this point. There was great divergence of opinion as to the animal's being in heat and the length of the period of heat. The opinion of the keeper apparently was based in large part upon the fact that Jap had this habit of sucking the breasts and that this was more intense at times than at others. The uncertain beliefs as to whether Jap had been in heat lead one to infer that her age is not so great as commonly stated (unconfirmed statements were she was 80 years old). However, as the evidence for the animal's being in heat is so contradictory, it can not be used as throwing any light on her probable age.

The Ringling herd, according to Doherty, show the presence of sexual activity only by a tendency to be a little more stubborn and less ready to perform as desired in the ring. Doherty is convinced that the sucking of the breasts has nothing to do with sexual excitement but is merely a habit, since many animals do this. The elephant's trunk is continually playing all over the body, and the fact that it is attached to the breast at times has no particular significance. McClain and Noble have observed no œstrus cycle in the case of the Barnes herd. Clark and Veasey, at

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[1] Evans, G. H., *Elephants and their diseases*, Rangoon, 1910, p. 94.

[2] Steel, J. H., *A manual of the diseases of the elephant and of his management and uses*, Madras, 1885.

Franklin Park in Boston, have never seen any evidence of the elephants there being in heat. One of them (No. 3) does aspirate the nipples occasionally, but Clark does not consider this a sign of heat. Neuffer, the trainer of elephant No. 4 at the Benson animal farm in Nashua, New Hampshire, says that this animal is in heat about every two months and at such times shows a tendency to excite the genitalia with the tail, by crossing of the legs, and pushing the genitalia toward the rear. At such times, also, the temporal glands are open and running.

Zukowsky's observations on the sex instinct in the elephant, based upon his long experience with the animals in the Hagenbeck Tierpark, have been communicated to us in a letter, with permission to quote in full. His comments are as follows:

> "Was nun Ihre Fragen über die Brunft des Elefanten anbelangt, so muss ich durchaus Ihre Meinung teilen, nämlich, dass sich die sogenannte 'Hitze' beim Elefanten nur in sehr geringem Masse zeigt und zwar so unwesentlich, dass selbst langjährige Pfleger oftmals diese Erscheinung noch nicht wahrgenommen haben, zumal sie bei den verschiedenen Kühen auch sehr verschieden stark auftritt. Als Ursache für die minimalen äusseren Brunftzeichen möchte ich mit Sicherheit annehmen, dass diese Erscheinung mit dem *Absterben des Elefantengeschlechtes,* das seine Blütezeit ja in der Pliozänzeit hatte, in Zusammenhang zu bringen ist, ausserdem aber kann sie als eine *Folge der immer mehr abnehmenden Lebensbedingungen gelten.* Es gibt ja auch einen *inneren Artentod,* der durch das Versiegen der lebenswichtigen Säfte hervorgerufen wird. Ich glaube niemals, dass alle Geschlechter, die vor der heutigen Tierwelt den Erdball einmal bevölkerten, durch katastrophale Umwälzungen vernichtet wurden, sondern sogar grösstenteils durch diesen 'inneren Artentod,' der durch vielerlei Erscheinungen hervorgerufen werden kann. Aber, wir kommen vom Thema durch solche weitschweifigen Betrachtungen zu weit ab."
>
> "Als Anzeichen der Brunft habe ich bei unsern Elefanten, wie Sie ja ganz richtig bemerken, geringere Bereitwilligkeit beim Arbeiten, Interesselosigkeit der menschlichen Umgebung gegenüber, leichte Erregbarkeit, schnellere Bewegungen und vor allem lebhafteres Rüsselspiel und Ohrenklappen feststellen können. Wie bemerkt, sind diese Merkmale bei den einzelnen Tieren in sehr verschiedenem Masse vorhanden, auch steht durchaus nicht fest, ob der eine Elefant die Merkmale zu jeder Brunft in gleichem Masse zeigt. Was die Dauer und die zeitliche Wiederkehr der Brunft bei den Kühen anbelangt, so habe ich hier die Wahrnehmung gemacht, dass unsre Kühe in Abständen von vier bis sechs Wochen brünftig werden. Die Dauer der Brunft beträgt etwa vier bis fünf Tage. Ein Laufen der Schläfendrüse habe ich bei den Kühen in sehr verschiedener Stärke beobachtet. Die Absonderung des Sekretes hängt offensichtlich von der Stärke der Hitze ab. Viele Kühe zeigen dann noch nicht enimal feuchte Stellen an der Ohrdrüse, während beim afrikanischen Elefanten, von dem nur geringe Beobachtungen vorliegen, die Drüse manchmal regelrecht tropft! Auch haben wir schon wiederholt Elefantenkühe hier gehabt, die zur geschlechtlichen Erregung ihre Genitalien an Wänden oder Stämmen scheuerten, auch verrieten sie häufig ihre Erregung durch seltsame Bewegungen der Hinterbeine. Auch Fälle regelrechter Onanie sind mir bekannt geworden. Es ist erklärlich, dass diese Erscheinungen durch die Haltung in der Gefangenschaft und den unbefriedigten Geschlechtstrieb hervorgerufen werden."

From the observations of Neuffer and Zukowsky it would appear that with some females the phenomenon of sexual urge is as pronounced as it is with many domestic animals. These rare instances may be explained by the youth of these elephants. But in general the adult elephant shows little, if any, indications of sexual excitement. Perhaps the circus elephants have reached an age at which the sex instinct is less intense, and that is the reason elephant men rarely notice any indications of sexual excitement among their elephants. Certainly the sex cycle plays no significant rôle in the yearly life of the average female circus elephant. Probably any such œstrus period is rarely recognized when it occurs. It may be that females will receive the male when not giving external evidence of intense rut.[1] From our personal experience with a large number of female elephants on exhibit in various circuses in the United States it is clear that there is rarely any evidence of heat and that most elephant men are unaware that their elephants are in heat. Thus it would appear that the sex activity, at least with the female elephant, is at an extraordinarily low level. Little evidence is available with regard to the males other than the general impression that in course of time they become unruly and have to be taken out of exhibits. This unruliness is associated, in general, with their sex life.[2]

Period of gestation—The fact that females have been known to receive the male even after they have supposedly become pregnant challenges seriously any individual estimates as to the precise length of the period of gestation. Common report places the period of gestation at not far from 18 to 22 months or, on the average, 20 months.[3] This is the general picture both for Indian and African elephants, based on many different observations, and is in all probability very nearly correct. (See table 4 for reasonably close estimates of the duration of gestation.)

Parturition of the Elephant

Perhaps the most noted case of breeding of an elephant in captivity, with reasonably careful records regarding the periods of gestation and with at least one accurate report of parturition, is that of "Princess Alice." [4] In the course of her life this elephant gave birth to four babies, all males. The fact that four baby elephants were born in captivity, having not only one and the same mother but the same sire, certainly is a record. In view of its great scientific and physiological importance, this experience has been imperfectly reported (chiefly in the newspapers). Heller gives a digest, which is in all probability reasonably accurate, regarding these births, although they were not actually observed by him. The brief statement by Grimpe[1] about these babies is apparently taken from Heller's report. Correspondence with a number of individuals associated at different times with one or more of these four births has revealed the fact that at the second birth an obstetrician, Dr. T. Mitchell Burns of Denver, Colorado, was present. He made a series of pertinent observations regarding the parturition, which he has kindly placed in our hands. The following is, in part, a paraphrase of Dr. Burns's report.

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[1] Schiött (Zool. Beobachter, 1908, **49**, p. 133) states that Ellen, the Copenhagen female, received the male frequently, even when pregnant.

[2] An heroic effort to castrate a recalcitrant male was made in 1889 by W. Shaw (Vet. Journ., London, 1900, N. S., **2**, p. 151). The animal lived but 57 hours after operation, but no necropsy was made to determine the cause of death.

[3] Chapman, H. C., Journ. Acad. Nat. Sci., Phila., 1874-1881, **8** (2d ser.), p. 413. Chapman comments on the fact that Aristotle stated the period of gestation was nearly two years. Corse, J., Phil. Trans. Roy. Soc. London, 1799, Pt. 1, p. 31; Evans, G. H., Elephants and their diseases, Rangoon, 1901 and 1910; Gowers, W., Proc. Zool. Soc. London, 1931, p. 1207; Turpin (***Histoire Universelle du Royaume de Siam,*** Paris, 1771, **I**, p. 265) states that the period of pregnancy lasts 12 months and that the baby sucks with its trunk for it can not reach the mother's breast with its mouth!!!

[4] Heller, E., Bull. Wash. Park Zool. Soc., Milwaukee, 1933, **4**, No. 1.

Cohabitation occurred some night between June 12 and sometime in September 1912. The exact time is unknown, as the male would get loose nights and roam around. If the period of gestation is timed from June 12 to March 28 (the date of the birth), this indicates 21½ months as the longest possible duration of the pregnancy, but if conception occurred in September, the period of pregnancy lasted about 18 months. On March 22, 1914, the rest of the herd to which this Princess Alice belonged left their winter quarters for the road. Soon after they had gone the female "apparently started in having regular 'pains' about every minute, *i.e.*, she would groan and pull and twist and at times seem to bear down a little, and the vulva would descend some. Her bowels moved many times, and she urinated every few minutes. Her eyes had a scared expression. She would tug at her chains, and at times she would try to break, with her head, a very strong cross beam above her. Towards evening she quieted, but it was many hours before she lay down. This was either a case of hysteria or false labor pains, brought on by the excitement produced by the leaving of the rest of the herd."

"On March 28, 1914, at 5.00 a. m., her keeper was awakened by the noise produced by her slapping the vulva with her tail, apparently to remove the mucus. Up to 9.40 a. m. she had had only about five good 'pains.' From 9.40 to 10.05 a. m. she had three strong pains. At 10.08 a. m. the first blood clot passed, and she laid her trunk on the ground. Shortly after this the blood began to come in a small stream, and this kept up, off and on, until the birth. She frequently slapped the vulva with her tail to remove strings of mucus which would hang down. Often she would twist from side to side. At other times she would put her trunk between her legs and push back, with her forelegs extended. With the real expulsive pains and when the birth occurred she doubled up, *i. e.*, she assumed the attitude the dog does in defecation, with trunk between forelegs and weight on hind legs. A long sac, shaped like an elephant's leg, projected from the vulva at the beginning of the last pain. It contained the left foreleg and was followed by the rest of the sac and the fetus, which was born at about 10.35 a. m. The baby was pulled from under the mother, who remained standing. The navel cord broke as the baby fell to the floor. The baby was soon wiped dry. There was no vernix caseosa or blood on him. He was just wet. He breathed and defecated at once. The amnion covered the body more or less." At 10.55 a. m. he was on his feet, but very unsteady. At 11.15 a. m. he cried. At 11.55 a. m. he walked very well, and urinated at 1.00 p. m.

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[1] Grimpe, G., Zool. Garten, 1933, 6, p. 196.

"At 12.40 p. m. pains for the after-birth began. The after-birth was expelled at 2.10 p. m., followed by a large amount of blood and clots. By the fall of the baby at its birth the cord was pulled off right close to the navel or, rather, just within the navel. The after-birth without the amnion and free of blood, except that in the cord, weighed 28½ pounds. In the cord there were two arteries and one vein, which branched. The after-birth consisted of three placentæ arranged zonary."

On March 29 the baby was allowed to go up to the mother, but the mother knocked him over into the corner, and later, when he went back of her, she kicked him over. When the baby was held up to her, she would try to lie down on him. The absence of maternal affection on the part of this female was noted in the case of all four of her babies. This elephant calf was neither weighed nor measured, but the weight was guessed at as 160 to 187 pounds. Its height was about 3 feet.

Of special interest in connection with the birth of this second baby is the fact that the animal was heavily furred. This statement, made by one of those present at the birth, is confirmed by an indistinct and possibly somewhat retouched newspaper photograph in the Denver Post of March 28, 1914. The fur is undoubtedly the retention of a juvenile characteristic, which is rapidly lost as the elephant grows.

Composition of Elephant's Milk

The earliest published analysis of elephant's milk is that reported by Doremus in 1882.[1] Three specimens of elephant's milk were secured by him, amounting to 19, 36, and 72 c.c., respectively. The specific gravity of the third specimen was 1.0237. The analyses show that the milk was more nearly the consistency of cream, since the fat content ranged from 17.5 to 22.1 per cent and the total solids from 30.7 to 33.3 per cent. Several unconfirmed reports hint that the milk of Princess Alice had been analyzed on several occasions, but no printed report in any regularly accredited journal has been found. Fortunately, owing to the kindness of Mr. Hugh W. Davy of Salt Lake City, Utah, we have received a photostat copy of a report of an analysis of this elephant's milk. The sample of milk was collected by Mr. Emil M. Schider, at that time the keeper of Princess Alice. The analysis was made by the then state chemist, Herman Harms, and his report, dated at Salt Lake City, Utah, June 7, 1918, was made to the State Board of Health at Salt Lake City. The sample of milk amounted to 25 c.c. and in consistency was rather a thin fluid. The results of the analysis are as follows:

Specific gravity (Picnometer method)	1.038
Reaction	Neutral
Fat (Rose-Gottlieb method)	3.89 p. ct.
Albuminoids and sugar	11.82 p. ct.
Ash or mineral matter	.47 p. ct.
Water	83.82 p. ct.
Total solids	16.18 p. ct.

The chemist records that "in comparison with the average cow's milk the elephant's milk shows a higher specific gravity and contains about 4 per cent more total solids. The proportion of fat is about the same in both."

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[1] Doremus, C. A., Med. News, Phila., 1882, **40**, p. 282.

Relationship of Weight of Baby to Weight of Mother

The data that have been found in the literature regarding the breeding of elephants in captivity, with particular reference to the length of the period of gestation, the weights and heights of new-born elephants, their length of life, and their weights at death, are summarized in table 4. The weights of the four babies of Princess Alice, although recorded in table 4, are uncertain. For the most part they are somewhat smaller than the reported weights of other baby elephants born in captivity. This is particularly striking when one considers that the weight of the mother (although extraordinarily varying weights are given for her) was in all probability not far from 8000 pounds. Although Princess Alice is still alive (December 18, 1935), she has not been weighed recently. Her height has been carefully estimated to be a little under 9 feet. The circumference of her right foot was accurately measured and found to be 51½ inches. Although this index of the probable height of the elephant is liable to be in error (see page 101), this measurement shows at least that Princess Alice is a large rather than a small elephant.

The average weight of the new-born elephant is not far from 220 pounds (100 kg.). On the assumption that the average adult female elephant (see table 2) would weigh about 6000 pounds (2700 kg.), the weight of the new-born baby is only about 3.5 per cent of the mother's weight. In the specific instances of the mothers Roma and Hebe, records of whose weights are available for comparison with their babies' weights, this percentage relationship was 4 and 3, respectively. This is a small percentage when one considers the relationships of weight of baby to weight of mother in the case of animals of other species. Thus with humans, the infant's weight of about 8 pounds (3.6 kg.) would be approximately 6 or 7 per cent of the mother's weight, and with domestic animals the percentage might be even larger, 10 per cent or over.

There is no authoritative information regarding the birth weight of whales. Krogh[1] has calculated from the remarkably constant relationship between the lengths and weights of whales as reported by Laurie that a new-born Blue whale 7 meters long would weigh about 2000 kg.[2] According to Laurie [3] an adult Blue whale captured at Stromness weighed 122,000 kg. Had this whale been the mother of a 2000-kg. baby, therefore, the baby would have weighed only 1.6 per cent of the mother's weight. The probable error in the calculation of the weight of the new-born whale might be considerable and yet not affect this percentage relationship appreciably, but an error in the mother's weight would have more of an effect. Thus if the mother

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[1] Krogh, A., Nature, 1934, **133**, p. 635. This calculation employed by Krogh was used by Pütter, who made a model of the whale. Pütter's calculations show the great chance for error in trying to compute the size of an adult animal from the length and general configuration of the fetus. (See Pütter, A., Zool. Jahrb., Abt. f. allg. Zool. u. Physiol., 1923, **40**, p. 217.)

[2] For extensive data comparing the lengths of mother whales and whale fetuses see S. Risting, Conseil Permanent International pour l'Exploration de la Mer, Rapports, 1928, **50**, 122 pp. See, also, length measurements reported by R. C. Andrews (*Whale hunting with gun and camera,* London, 1916, pp. 73 and 113).

[3] Laurie, A. H., *Some aspects of respiration in blue and fin whales, Discovery* Reports, 1933, *7*, p. 363.

TABLE 4—*Data on weights of new-born elephants and length of life*

Mother, age, and weight	Gestation period	Name	Place of birth	Date of birth	Sex	Weight at birth	Height at birth	Length of life	Cause of death
						kg.	*cm.*		
Name unknown[1]	21 to 22 mos.	....	....	....	F	96.8	76	....	
Hebe[2], 23 yrs. 3175 kg.	....	....	Philadelphia, Pa.	Mar. 10, 1880	?	97.1	89	25 yrs.	Became a killer, so sacrificed.
Queen[2]	....	....	Bridgeport, Conn.	Feb. 2, 1882	?	....	....	5 yrs.	Burned to death in fire.
Ellen[3] ca. 13 yrs.	24 mos.	Kaspar	Copenhagen, Den.	Dec. 9, 1907	M	....	....	19 yrs.	Strangled in his pen.
	21 mos. 27 days	Julius	" "	Apr. 6, 1912	M	....	....	9 yrs.	Blood poisoning from scratch on face.
	22 mos.	Lauritz	" "	Apr. 3, 1916	M	138	....	23 days	Lost weight constantly, so killed.
Princess Alice[2] ca. 27 yrs. (?) 3600 kg (?)	21 mos.	Hutch	Salinas, Calif.	Apr. 25, 1912	M	81.6	71	6 wks.	Early mortality perhaps due to mother's not nursing babies. Hutch died as result of a shake-up in a train wreck.
	20 mos.	Tambon	Denver, Col.	Mar. 28, 1914	M	72.6	....	27 days (?)	
	18 mos.	Little Miracle	Denver, Col.	Mar. 16, 1916	M	73.5	....	6 mos.	
	21 mos.	Prince Utah	Salt Lake City, Utah	Apr. 29, 1918[4]	M	77.1	....	10 mos.	
Jenny[5] 22 yrs.	21 mos. 18 days	....	Budapest, Hungary	Jan. 12, 1930	F	86	83	....	Trampled to death, after birth, by mother.
	20 mos. 27 days	....	" "	Dec. 27, 1932	M	91.5	92	....	
Roma[6] 3340 kg.	....	Minjak	Essen, Germany	Jan. 29, 1932	F	127	90	....	
Cora[7], 9 yrs.	....	....	Munich, Germany	May 1932	F	50	81	....	
Name unknown[8]	....	....	....	1929	....	ca. 113	90	....	
Name unknown[8]	....	....	....	1932	....	ca. 113	90	....	

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[1] Chapman, H. C., Journ. Acad. Nat. Sci., Phila., 1874-81, **8** (2d ser.), p. 413.

[2] Heller, E., Bull. Wash. Park Zool. Soc., 1933, **4**, No. 1. (See also, G. Grimpe, Zool. Garten, 1933, **6**, p. 196.)

[3] Schiött, J., Zool. Beobachter, 1908, 49 Jahrg., p. 133; Hvass, H., Zool. Garten, 1932, **5**, p. 191.

[4] According to a birth certificate issued by D. A. Beeman, registrar of vital statistics, Salt Lake City, Utah.

[5] v. Anghi, C. G., Zool. Garten, 1934, **7**, p. 68.

[6] Schneider, K. M., Zool. Garten, 1933, **6**, p. 144.

[7] Antonius, O., Zool. Garten, 1932, **5**, p. 170.

[8] Personal correspondence from Dr. Ludwig Zukowsky of the Hagenbeck Tierpark, Hamburg, Germany.

weighed 80,000 kg. instead of 122,000 kg., the baby's weight of 2000 kg. would be 2.5 per cent of the mother's weight instead of 1.6 per cent. The percentage relationship, however, is probably the smallest with the whale, about 2 per cent, next smallest with the elephant, 3 or 4 per cent, and next in order with humans, about 7 per cent. In other words, the weight of the baby in proportion to the weight of the mother increases, in general, inversely with the size of the mother.

A number of striking exceptions to this generalization should be called to attention here, although the subject can by no means be completely investigated. It is well known that a Holstein cow produces unusually large calves. Dean L. S. Corbett of the Department of Animal Industry at the University of Maine has kindly given us information regarding the birth records of their Holstein cows. One weighing 1730 pounds (785 kg.) gave birth to a calf weighing 132 pounds (60 kg.) or a little under 8 per cent. It is thus seen that with the cow, which weighs many times what the average woman weighs, the relationship of baby's weight to mother's weight is not less than this relationship with humans, which is about 7 per cent. Another striking exception is the relationship noted between a mother bear and a baby bear born during hibernation, the weight of which was but a fraction of a per cent of the weight of the parent. Thus a baby bear born at the New York Zoological Park, full term, weighed 14 oz. (0.4 kg.) and the mother weighed 500 pounds (227 kg.). This, however, is perhaps the most extreme case among captive animals.

Breeding of Elephants in Captivity

In view of the total number of adult elephants in captivity, the number of young born seems extremely small, suggesting that elephants do not breed readily in captivity. Thus, the elephant born in Munich in 1932 was stated to be the ninth born in captivity in Europe,[1] and the elephant born in the Cooper and Bailey Menagerie at Philadelphia, Pennsylvania, on March 10, 1880, is maintained to have been the first born in America since prehistoric times.[2] One reason for the neglect of breeding in captivity is that the elephant is nearly twelve years of age before it becomes sexually mature, and in India and Burma at least they can be captured in the wild in the adult stage. Another reason for relatively rare mating in captivity is that the males are classed as dangerous animals, having demonstrated their viciousness and intractability for circus life. Furthermore, it is a not uncommon experience with many animals in parks that the male may actually damage, if not indeed kill, the female. One of the most successful matings in captivity was that of Ellen at the Copenhagen Zoological Park, who gave birth to three infants.[3] Although Hvass states that this was a record, it has actually been surpassed by the births of Princess Alice at the Denver Zoological Park and later at the Salt Lake City Zoo, who gave birth to four babies, all sired by one male, Snyder. The male became intractable and was shot twenty years ago, but Princess Alice is still living and is estimated to be about 50 years of age.

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[1] Antonius, O., Zool. Garten, 1932, **5**, p. 170.

[2] Zipperlen, A., Zool. Beobachter, 1880, **21**, p. 96.

[3] Schiött, J., Zool. Beobachter (Zool. Garten), 1908, **49**, p. 133; Hvass, H., Zool. Garten, 1932, **5**, p. 191.

All the babies of Princess Alice died within one year's time. Most of the births recorded in table 4 occurred fifteen or more years ago, when the feeding of animals in captivity was on a much less scientific basis than it is at the present time. In those days animals bred in zoological parks almost invariably suffered from rickets. As a result of modern ideas regarding vitamines, salts, ultra-violet light, and similar factors, the artificial rearing of young wild animals has been revolutionized, and without doubt the short-lived elephant babies in the earlier days could have been saved by modern methods of care. It is, however, a fact that most elephants born in captivity do not live for a normal length of time. This very fact has probably deterred the breeding of elephants. It is uneconomical to breed them as working animals, since they must be at least twelve years old before they are of any value, and full-grown adults can be easily captured. From the standpoint of circuses and exhibitions baby elephants are great attractions. The fact that the baby elephant is seldom exhibited at the present day indicates, however, that the tendency for breeding in captivity is even less than in former years. In future experience with elephants in captivity, if more attention is paid to the scientific feeding, first, of the adults prior to mating, then of the female during pregnancy and lactation, and finally of the young during and after nursing, reproduction and the growth of young may be far more successful than has thus far been the case. Unquestionably special emphasis should be laid upon the relationships between feeding, fertility, milk production, and growth, and the importance of factors today recognized as of utmost importance in human reproduction and growth.

HEARING

Any one who is continually about elephants realizes that they are rarely spoken to except in very loud tones. It is the practise of elephant keepers to yell at their animals. This may be part of the exhibition at an animal show, to convey the impression that a massive animal needs powerful commands, or there may be a real feeling on the part of the keeper that the elephant will not pay attention or can not hear. Observations on Jap led to the conviction that this animal has a keen sense of hearing. The writer personally never spoke to her except in a moderate tone of voice. The various keepers and attendants in and about the barn invariably yelled at her at the top of their lungs. One indication that Jap might have extreme sensitivity of hearing was given during the series of respiration experiments. In these tests it was necessary every half hour for one of the observers to climb to the top of the respiration chamber by a 4-meter ladder, to read the thermometer in the top of the chamber. The ladder was carefully placed with the lower end embedded in the earth of the barn floor and the top resting firmly against one of the barn timbers. In mounting the ladder, the observer moved quietly and had rubbers on his feet. Every time he went up, however, the keeper inside called, asking if the thermometer was being read, for Jap invariably turned her head and body toward the corner where the thermometer was. Since an electric fan was in motion inside the chamber and the noise from the ventilation blowers was fairly great, this extreme sensitivity to a slight superimposed sound was marked. When chained in the barn, Jap could hear the keeper coming across the road with a forkful of hay long before she could see him.

Most of the junior keepers of the Ringling herd yelled at their animals. Doherty, however, the head keeper, spoke in a well-modulated voice, and none of the other keepers were obeyed with the instantaneous response that followed his commands. The conclusion is that the elephant, even in captivity in the excitement, noise, and clatter of the circus, has extremely sensitive hearing.

PHYSICAL APPEARANCE OF THE ELEPHANT JAP

Jap challenged our attention on account of her size and generally fine appearance. In many ways she compares well in appearance with the majority of the famous Ringling herd and the Barnes herd, although far from being so well groomed. The only external physical imperfections are the mutilated ears, especially the right ear.[1] It is reported that this ear had been frozen, and the frozen part sloughed off. To a certain extent this is true of the left ear. This report concerning the frozen ears gives a hint as to the extreme temperatures to which this beast has been subjected. In common with the other sixty-two elephants that we examined, Jap had the usual five toenails on each front foot and four on each rear foot.

RESISTANCE TO COLD

From the fact that the elephant is a tropical or sub-tropical animal and that it is essentially hairless, one would infer that it has no great resistance to cold. The heavy loss of elephants that Hannibal experienced in crossing the Alps was without doubt due to the ravages of severe cold and not, as has so frequently been thought, to the roughness of the terrain, for Sanderson[2] speaks of "some terrible distances which no beast of burden but an elephant could have managed" and states that "Elephants rarely stumble; should they even do so, they never fall from that cause as they can go down on one or both knees—an easy position for an elephant."

In most zoological parks the temperature of the elephant house is kept at not far from 20° C., which is considered the optimum temperature, and the elephants are not allowed outdoors in cold weather. When it was proposed to several park men that an elephant be taken outdoors on a frosty morning to note whether there was any exhalation of air from the mouth during respiration, such a test was denied. With the Ringling herd precautions are taken against drafts, and constant watch is maintained to insure that the elephants are not subjected to any unusual and sudden temperature changes, for it is current belief that elephants are sensitive to cold, will catch cold easily, and die of respiratory infections.[1]

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[1] See the insert in the retouched newspaper photograph reproduced in Plate 3B, page 34. The significance of the ear in identifying Jap played an interesting rôle in our study. After our experiments were completed, it was found that certain of Brody's data on elephants, although numerically far from agreeing with our results (see page 240), suggested that one of the elephants he had worked with in August 1932 might have been Jap, the elephant that we studied. This was finally proved by noting the outline and pigmentation of the left ear, for fortunately we had a good photograph of that side of the elephant taken by Professor Brody to compare with our own photographs of Jap. Several months later we made contact with the trainer who had charge of the elephant at the time Brody used her, and he verified completely our finding that she was one and the same animal. This comparison of the ears of elephants is comparable to the finger printing of humans.

[2] Sanderson, G. P., *Thirteen years among the wild beasts of India*, London, 2d ed., 1879.

In striking contrast to this almost universal custom of circuses and zoological parks of keeping their elephants warm or at least not chilled, almost complete indifference was shown in exposing Jap to severe cold, and this animal possessed an extraordinary resistance to cold. Jap's experience in the fall of 1934 illustrates well the extremes in temperature to which she was subjected. For several weeks she had been kept in the steam-heated basement of the New York Hippodrome, at a moderate temperature. She was then moved to a cellar stable on 42d Street, unheated, unventilated, and poorly lighted. The stable was cold (about 40° F.) and it was uncomfortable there for a man, even with an overcoat on. The only protection that Jap had against the cold there was a canvas blanket that was wrapped around her body, but not over the head, ears, or trunk. The sudden transfer from the steam-heated quarters of the Hippodrome to the unheated stable must have made the change in temperature seem pronounced, and yet Jap was apparently unaffected. During that fall and part of the winter she was on the streets of New York almost every day, bearing an advertising placard but otherwise unprotected. For this advertising campaign she was transported back and forth between Campgaw and New York daily, 30 miles, in an open truck, with no protection of any kind other than the canvas blanket.

In the stable at Campgaw two provisions were made to protect Jap against the cold. In the first place, a canvas blanket was used, at least during our first series of observations. This blanket, however, was pulled off by Jap on the fourth day (March 11) of the first series of tests and was not put on thereafter, either during the remainder of the first or during the second series. On the days when Jap was inside the respiration chamber, the blanket was worn only once (March 10). All subsequent tests were made without the blanket. Second, there was heat from the small stove in one corner of the barn, but it is believed that the fire built there was fully as much for the comfort of the keeper and the assistants who gathered there as it was for the comfort of Jap. The elephant stood (Plate 2A, page 30) directly in front of the barn doors. These were not entirely tight and much cold air could flow in around them. During the respiration experiments at Campgaw a recording thermometer was fastened on the outside of the chamber (Plate 6, page 56) at about the height of the elephant's shoulders. This thermometer indicated probably not far from the temperature of the air at this level, although without doubt Jap was much colder, for she stood near the barn doors and the thermometer was some distance from the doors. On four nights (March 9-10, March 13-14, March 14-15, and March 17-18) the temperature as recorded on this thermometer reached 0° C. (32° F.)

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[1] While on tour, to protect the Ringling elephants against possible chilling, four blankets are generally carried, and these are usually applied to the older animals, such as Nos. 18 and 42, who feel the cold more. Once during the 1935 tour it was found necessary to put the four blankets on four elephants, and a number of the other animals were covered with patched-up canvas and other pieces of cloth.

and remained at this level for several hours, on one occasion (March 9-10) for seven hours, and on one night the water in the water seal of the blower box froze. During the second series of observations at Campgaw, when Jap wore no blanket at any time, the barn temperature was read nearly every two hours on a mercurial thermometer and on many occasions was found to be as low as 8° C. (See table 16, page 143.) In no instance during the entire nine days of this second series of measurements was the barn temperature above 17° C. The average temperature for the day and night was 12° C.

The only times when Jap showed any reaction to cold were shortly after she drank a large volume of water, when she shivered and appeared to suffer discomfort. In New York the water given to her had been warmed and, in fact, was almost hot, but in Campgaw she was given water directly from the faucet, which had a temperature of from 7.5° to 12.1° C. There must have been a great absorption of heat from the elephant's body to warm suddenly the large amounts of cold water that she drank,[1] and it is not strange that she shivered and showed signs of distress.[2] This evidence of discomfort, however, was only of short duration and was given no attention by the attendants.

This particular elephant, a tropical, hairless animal, was, therefore, living much of the time in an environment at such a cold temperature that the assistants, well clothed though they were, felt uncomfortable if they sat still in it even for a few moments. The only times that Jap was at an environmental temperature approximating that prevailing in elephant houses in zoological parks, about 20° C., was during the period of 4½ hours spent inside the respiration chamber during each metabolism experiment. Then her own body heat, which was partly conserved by the walls of the chamber, warmed the air of the chamber usually to about 20° to 25° C. Hence from the standpoint of resistance to cold, Jap may be said to be an unusual animal, comparable perhaps to the artist's model inured to cold, who has been studied so much at the Nutrition Laboratory.[3]

In our search of elephant literature we have nowhere found record of any elephant having such immunity to cold as was shown by Jap. The question naturally arises as to whether this is a peculiarity of this elephant resulting from her frequently changing occupations, the various methods of transporting her, the economic necessity of curtailing the artificial heating in the buildings where she was housed, and the frequent underfeeding. Experiments with humans have shown that men subjected to undernutrition became more sensitive to cold,[1] and it is reasonable to presume that a normal animal would be affected in the same manner. Whether any other elephant could be hardened or trained to extreme cold is debatable. Because of the expense of these animals and the supposed danger to them of respiratory infection, it is unlikely that such an experiment will be designedly carried out in the near future. Studies have shown that the pre-historic elephant had a heavy coating of fur, and it is not impossible that Jap's resistance to cold may be an inheritance from an earlier race of elephants that were more protected against external conditions by their fur covering. This seeming indifference of Jap to environmental temperature assumes importance in the discussion of the respiration experiments on this animal (see pages 269 to 271).

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[1] Cannon and his colleagues have reported that the introduction of known amounts of cold water having a temperature of from 0° to 1° C. into the stomachs of cats with denervated hearts resulted in a "heat debt" (extra heat which the organism must produce to maintain its own temperature) of between 1500 and 2000 small calories per kilogram of body weight. See Cannon, W. B., Querido, A., Britton, S. W., and E. M. Bright, Amer. Journ. Physiol., 1927, **79**, p. 466.

[2] This experience of being chilled after drinking water was likewise noted in one of the older elephants in the Ringling herd at Sarasota. After drinking a large amount of water, at a temperature of 23° C., elephant No. 42 gave evidence of being chilled, mostly noticed by "jumping" (as it was called by the elephant men) in the throat. Doherty ordered that she be immediately warmed up by exercise in the ring. The hint from these two experiences suggests that it is desirable to give elephants warm (preferably fairly warm) water, when possible.

[3] Benedict, F. G., and M. D. Finn, Amer. Journ. Physiol., 1928, **86**, p. 59; Benedict, F. G., Amer. Journ. Physiol., 1928, **85**, p. 650; Benedict, F. G., Asher-Spiro's Ergebnisse der Physiol., 1925, **24**, p. 594.

That environmental temperature at which an animal does not increase its heat production to combat cold is called the "critical temperature." What is the critical temperature of the elephant? This varies greatly with different animal species. With the rat and, indeed, most animals it is not far from 28° to 30° C. With the goose, with its heavy protection of feathers, it extends from 28° down to 15° C., and the range from 15° to 28° C. is termed the "zone of thermic neutrality" of this animal. The steer apparently is not affected by a cold temperature down to 10° or 11° C., and the zone of thermic neutrality of the sheep with its heavy wool covering extends nearly to 0° C. The elephant, because a hairless animal, would *a priori* be expected to have a high critical temperature. However, it is characteristic of all animals studied much below the critical temperature to have obvious indications of combating cold, either in erected hairs or feathers in the case of furred animals or birds, or shivering in the case of the poorly covered or hairless animals. The complete absence of shivering by Jap other than following the drinking of cold water suggests that her zone of thermic neutrality may be very wide. Unfortunately our experimental program could not contribute to this important physiological question.

PHYSICAL CHARACTERISTICS[2]

Because the elephant is the largest living terrestrial animal, its gigantic size has always awakened general interest, but accurate statements as to its size (expressed either as height or weight) are difficult to find. The chief reason for this lack of accurate statement is that elephants are used in large part for show purposes and consequently their dimensions are never minimized, the owners too often exercising the inalienable right of the old showman never to underestimate. The size of the elephant has been expressed in various terms of weight, height, girths, and lengths, but the height has been emphasized from the earliest dates. In the early literature there are frequent references to the height of these animals (and these grossly exaggerated), but certainly up to 1843, that is, up to the time when the book of Armandi was published, no weights were recorded. The ancients had no adequate methods for weighing animals of this huge size, and consequently expressed the relative size of such animals in the fairly easily measured height. The ancients, however, were not the only ones who experienced difficulties in weighing massive animals. One finds even in the modern literature frequent references to the difficulty of determining the weights of large animals, notably the whale. This has been emphasized by Pütter[1] and especially those studying the whale on the "*Discovery* expeditions." (See page 286.)

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[1] Benedict, F. G., Miles, W. R., Roth, P., and H. M. Smith, Carnegie Inst. Wash. Pub. No. 280, 1919.

[2] When this monograph was in galley proof, we received the most important and comprehensive paper of Dr. Glover M. Allen, entitled *Zoological results of the George Vanderbilt African Expedition of 1934. Part II—The Forest Elephant of Africa,* Proc. Acad. Nat. Sci., Phila., 1936, **88**, pp. 15-44. Although dealing almost exclusively with the African elephant, nevertheless Allen's report contains much information with regard to the history, habitat, age, size, period of gestation, rate of growth, and particularly the cranial characters, with emphasis on the dentition, all points bearing in part upon Indian as well as African elephants. The reader should consult Allen's article especially for literature on the Pigmy and the African elephant.

Our chief interest in the physical characteristics of the elephant is that we wish ultimately to compare the metabolic activity of the elephant with the metabolism of other animal species much smaller in size. For this purpose measurements of the mass and linear dimensions, particularly the height, are of special value, for metabolism investigators are always seeking some common basis for correlating the heat production or vital activity with some anatomical measurement. Thus, length might properly be compared to the "sitting height" as measured by Pirquet.[2]

It is obvious that in any scientific report only carefully attested linear measurements can be used. Hence much of the information available from many elephant men and non-critical writers must be disregarded. We are certain of the measurements actually made by us, which include the measurements of weight and height of Jap and the heights of all the Ringling elephants, as well as the heights of Tony and Waddy at Franklin Park. As regards the weights, we are certain only of Jap's and those obtained on the Ringling herd at Sarasota. These were actually recorded on scales. The weights of the other elephants, as given to us, are as "estimated" by the various keepers. In a number of instances these weights were accurately copied from records in notebooks, which give every evidence of being careful transcripts of truly attested weights. In a number of other cases they obviously represent "estimates." The true evaluation of these "estimated" weights is at best difficult, but in reporting the weights in table 2 (see page 22) we have disregarded those that appear wholly impossible and retained only those that seem to be within reasonable bounds. This procedure was strictly followed with the elephants studied in this research. Obviously, in quoting the literature, we have no alternative than to give the measurements as reported, but, as will be seen from the comments, these are frequently challenged.

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[1] Pütter, A., Zool. Jahrb., Abt. f. allg. Zool. u. Physiol., 1923, **40**, p. 217.

[2] Pirquet, C., *An outline of the Pirquet system of nutrition,* Phila. and London, 1922; *idem, System der Ernährung,* Berlin, 1917-1920, vols. 1-4; *idem,* Zeitschr. f. Kinderheilk., 1916-1918, vols. 14-18.

Height

ELEPHANTS' HEIGHTS RECORDED IN THE LITERATURE

The earliest records of the elephant's size are the heights given by Pliny the Elder,[1] who comments on the fact that the African elephant is not so large as the Indian elephant, but that in Ethiopia they are of equal size. He reports the height as "20 cubits." For the most part the records of height in the early literature are based on such inaccurate measurements and are so surrounded with erroneous statements as to make them of no real value. Furthermore, when these earlier reports of height are given in the classical literature, the precise translations of the early measurements into the metric system are often debatable. For example, the English expressions "hundredweight" and "quarter" do not mean 100 pounds and 25 pounds. "Hundredweight" means one-twentieth of a long ton or one-twentieth of 2240 pounds, which equals 112 pounds, and the "quarter" represents one-fourth of this or 28 pounds. The impressive, gigantic size of the elephant lends itself readily to overestimate of size by the inaccurate eye. The literature contains statements of elephants exceeding 14 or 15 feet in height, but reputedly accurate (?) measurements rarely give the height as 11 feet.

Many of the greatest heights recorded are those of males that have been killed in the forest and measured "in the field." These measurements, unchecked, have been made by the hunter with certainly no desire to minimize the size of his kill. Furthermore, the animal killed has always been measured lying down. Measurements under such conditions are always greater than those taken of a live animal while standing. It is almost impossible to adjust any animal of this massive size so as to have the tension on the muscles and bones the same as when it was alive. These observations reported by hunters in the field must be here disregarded.

Sanderson[2] records not having seen one 10 feet in vertical height at the shoulder. The largest was 9 feet 10 inches high (apparently a male). The largest females he had measured were 8 feet 5 inches and 8 feet 3 inches, respectively, and of one hundred and forty elephants captured by him, the tallest females were just 8 feet (vertical measurements at the shoulder). The largest height recorded for the male elephant, according to Evans, is 9 feet 10 inches and for the female 8 feet 5 inches, measured at the shoulder.

Measurements of elephants in captivity should obviously be much better made than those of elephants in the field. Of the very large elephants in captivity in the United States during the last fifty years, one thinks first of the widely exploited Jumbo. Although we hesitate to cite a popular magazine in a monograph of this type, nowhere are the difficulties of accurately measuring the height of the elephant, especially after death, better considered than in the article by Walter Guest Kellogg in a small booklet entitled "The Circus Scrapbook," for April 1932. Here, citing statements from Dr. William T. Hornaday, the former director of the New York Zoological Park, Kellogg brings out clearly the inconsistencies in the claimed and recorded heights of Jumbo and other large elephants. Bolivar, who was for many years at the Philadelphia Zoological Garden, was a giant Indian male, whose height at the time of death was 10 feet.[1]

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[1] Pliny, the Elder, *Natural Histories*, Book VIII.

[2] Sanderson, G. P., *Thirteen years among the wild beasts of India*, London, 2d ed., 1879, p. 55.

Kartoum, a gigantic African male that died at the New York Zoological Park a few years ago, was most carefully measured by Dr. W. Reid Blair and Dr. C. V. Noback. The heights of Kartoum were obtained from time to time to indicate his rate of growth.[2] Since they were always accurately obtained by an engineer with a surveying instrument, they are recorded in table 5. Kartoum's maximum height of 10 feet 8½ inches corresponds to 3.26 meters. If the circumference of the front hoof (4 feet 7½ inches—see table 7, page 103) is multiplied by 2 to obtain the height, in accordance with the popular method of calculation, this gives a height of but 9 feet 3 inches as compared with the height of 10 feet 8½ inches most carefully measured.

TABLE 5—*Heights of the male African elephant Kartoum*

Date	Height at shoulder	
	Feet and inches	Meters
Born 1903	....	....
Arrived at Park June 25, 1907	4 9½	1.46
Feb. 1, 1908	5 1¾	1.57
Nov. 1, 1908	5 2¾	1.59
Jan. 1, 1911	6 3	1.91
July 1, 1918	9 1	2.77
Jan. 1, 1921	9 3	2.82
Dec. 28, 1922	9 7¼	2.93
Jan. 1, 1924	9 9¾	2.99
Feb. 17, 1925	10 2	3.10
Jan. 21, 1926	10 3	3.12
July 13, 1926	10 5½	3.19
Dec. 31, 1927	10 6¾	3.22
Jan. 17, 1929	10 7½	3.24
Dec. 30, 1930	10 8½	3.26

In his account of the so-called "exiled elephants" on the island of Santa Rosa, Stock[3] reports that, according to fossil records of the mainland of California, elephants in that region ranged in height from approximately 10½ to 13½ feet, as measured at the shoulder. With due allowance for the difficulties of measuring animals in the lying position and particularly fossil animals, it is obvious that these early elephants were much larger than either of the two present-day predominant races, *Elephas africanus* and *Elephas indicus*.

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[1] Information given to us directly by the Zoological Society of Philadelphia.

[2] The changes in height accompanying growth were studied also by Schmidt (Zool. Garten, 1884, 25 Jahrg., p. 4) in a series of measurements on the same elephant during the period from 1863 to 1883. The elephant was 14 years old at the start. Schmidt reports numerous other measurements along with the records of height to indicate the yearly rate of growth. His tallest elephant had a height of 2.60 meters. Hundley (Proc. Zool. Soc. London, 1934, Pt. III, p. 697) reports the heights of Indian elephants during growth, based on findings on 220 males and females from one year to twenty-six years of age.

[3] Stock, C., Scientific Monthly, Sept. 1935, p. 205.

In this consideration of height, elephants of particularly large size have been emphasized. The statements that elephants may have a height of as much as 20 feet (6 meters) Evans says are extravagant, for twenty feet is essentially double the height of the tallest elephant. So far as the average sized elephant is concerned, Corse[1] (who for five years was director of elephant hunters in Tiperah, a province of Bengal in Asia) states that in India the height of the females is in general from 7 to 8 feet and that of the males from 8 to 10 feet, measured at the shoulder. Evans found that the average height of 300 male elephants was 7 feet 10½ inches. That of 100 females was 7 feet 5¾ inches at the shoulder, and only four had a height of 8 feet (2.4 meters) or over. The largest female was 8 feet 3 inches (2.5 meters) in height and weighed 2856 kg. Extremely large elephants such as those mentioned in the preceding paragraphs are usually males that are intractable and hence not suitable either for government service in India or for traveling circuses. These find their way, often years before they are shot, into zoological parks where they can be given every care, with precautions against any possible damage they may seek to do. This probably explains why the unusually large specimens are found in parks. All these extremely tall elephants, the heights of which have been recorded, were males.

METHODS OF MEASURING HEIGHT EMPLOYED IN THIS RESEARCH

The problem of measuring the height of the elephant is almost as great as that of securing proper weights. The exact location for recording the height has not until fairly recently been agreed upon, but at the present time practically all elephant men measure the height at the shoulder, much as is the custom in measuring the height of the horse. That the height at the shoulder does not by any means represent the highest point of the elephant in many cases is strikingly brought out by the observations of Schmidt.[2] In a series of measurements made on the same elephant in 1864, 1870, and 1883, the highest point of the back from the ground was, respectively, 2.35, 2.63, and 2.82 meters. The shoulder heights measured at the same time in the same years were 2.20, 2.43, and 2.60 meters, or essentially 20 cm. lower. The accurate measurement of the height of the elephant is not simple. It practically demands the skill of an engineer. Early recognizing this difficulty, elephant men have tried other methods of determining the height. The two more popular methods are still in use today. One is to measure the maximum circumference of the right front foot and to consider that this represents exactly half of the height of the elephant at the shoulder. The second is that employed at times of throwing a tape over the shoulder, measuring the entire distance from the outside of one front foot over the shoulder to the outside of the other front foot and dividing the result by two. This obviously gives a height considerably higher (probably 8 inches) than that represented by the direct perpendicular from the highest point of the shoulder to the ground.

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[1] Corse, J., Philos. Trans. Roy. Soc. London, 1799, Pt. I, pp. 31 and 205.

[2] Schmidt, M., Zool. Garten, 1884, **25**, p. 4.

Of these two methods, that of multiplying by 2 the measured circumference of the right foot is most popular. The blind faith in this method shown by many elephant men led us to expect fairly close agreement between such measurements and the heights at the highest point of the shoulder, but it was soon noted that the actual circumference of the foot was greatly affected by the weight borne by the animal on the foot at the time it was measured. A number of elephants were measured when the weight was on the foot and then when the weight was off, by having the foot lifted. In every case there was a shrinkage in circumference of from 1½ to 3 inches when the foot was lifted. Since this circumference is to be multiplied by 2, this comparison shows instantly that there is an inherent error of from 3 to 6 inches in this method of calculating the height of the elephant. Although this shrinkage in circumference was measured when the entire weight of the elephant was removed from the foot, there was a shrinkage in similar proportion, as far as we could estimate, according to whether the weight was equally distributed on both front feet or not. In other words, there is an inherent error in height measurements based on the measurements of the circumference of the foot. For purposes of comparison, however, with heights determined by other methods, measurements were made of the circumference of the right foot when the animal was standing on it in the case of the elephant Jap and elephants Nos. 2 and 3 and Nos. 14 to 63, inclusive.

Obviously the most scientific and only really correct method of measuring the height requires the services of an engineer with surveying instrument for establishing levels, as was done in the New York Zoological Park by Dr. W. Reid Blair in measuring the large animals there. To approximate this type of measurement, a simple apparatus was devised by us, consisting of a sliding rod, A, with a right-angle arm, B, at the top and provided somewhere along its length with a simple plumb bob, C, to insure that the rod is held in a vertical position when the measurement is made. This device is illustrated in figure 6. When the cross arm just touches the top of the shoulder, the two upright bars are firmly gripped in the hands to prevent the rod, A, from sliding, and the device is removed from the neighborhood of the elephant. The level of the lower end of rod A can then be read carefully at leisure, on the scale at the side of the upright A.

HEIGHT OF THE ELEPHANT JAP

Although Jap presented the appearance of a very large elephant, accurate measurements of her height were a part of the physiological picture. Our early experiences in attempting this measurement are so characteristic of the difficulties encountered, and in all probability have so often been duplicated by others, that they seem worthy of record. At the time of the experiments with Jap at Campgaw suitable engineering appliances, and especially the simple device illustrated in figure 6, were not available, and measurements of her height then were at best unsatisfactory. They illustrate strikingly, however, how anyone, even though desirous of most accurate measurements of the height, can be in error. At that time we did not clearly recognize that the height should be measured at the shoulder. Jap's *maximum* height was recorded, therefore, which in her case was at the top of the head. To get this height, one of the observers stood on a stepladder and laid a straight rod across the top of her head. The rod was supposedly levelled and sighted across the barn against the wall. One such measurement showed that Jap had an apparent height at the top of the head, in the ordinary position, of 9½ feet or 2.9 meters. This was wholly in accord with our impression that she was a large animal, but also suggested a height much greater than reported for other female elephants, and we were certain that she was not the tallest elephant we had ever seen. Arrangements were made subsequently with Engineer A. H. Ackerman of Campgaw to determine accurately the height of Jap at the shoulder. His measurements were carefully checked and show that her height at the shoulder is 8 feet 1 inch. The difference of nearly 1½ feet between the measured height at the shoulder and that estimated by us at the top of her head is probably much larger than actually obtains, but we have every confidence in Engineer Ackerman's measurement of the height, which can be stated to be 8 feet 1 inch, or 2.5 meters. Subsequent measurement of Jap's height at the shoulder with the device constructed at the Nutrition Laboratory showed perfect agreement with Engineer Ackerman's measurement. This apparatus was, therefore, used in our subsequent study of the heights of the Ringling elephants and Nos. 2 and 3. (See table 6, page 98.)

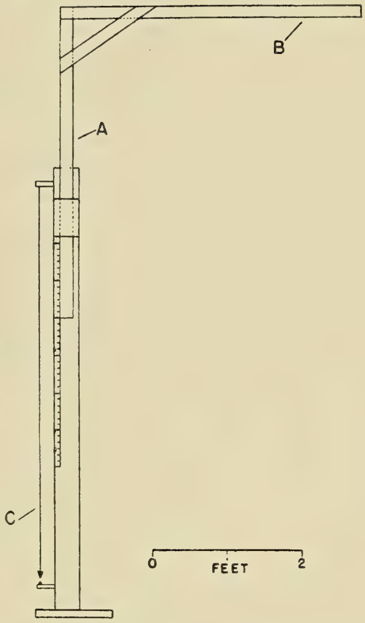

FIG. 6—DEVICE FOR ACCURATE MEASUREMENT OF ELEPHANT'S HEIGHT AT SHOULDER.

By means of the sliding rod A the right-angle cross arm B is adjusted to the highest point of the elephant's shoulder. The plumb bob C insures that the rod A is held in a vertical position.

COMPARISON OF THE HEIGHTS OF ELEPHANTS AS MEASURED BY THREE METHODS

In table 2 are recorded the heights of the several elephants upon which one type of observation or another was made. For Nos. 1 to 3 and Nos. 14 to 47, inclusive, the heights were measured by us by use of the device illustrated in figure 6. The height of No. 4 was given to us by her trainer,

Table 6—*Comparison of methods of measuring the height of the elephant*

Elephant No.	(a) Height at shoulder[1]	Half the distance over the shoulder from ground to ground				Twice the circumference of right front foot[2]			
		(b) As measured	(c) Deviation from shoulder height	Corrected for average deviation		(f) As measured	(g) Deviation from shoulder height	Corrected for average deviation	
				(d) Meters (b–19)	(e) Per cent of shoulder height			(h) Meters (f–5)	(i) Per cent of shoulder height
	meters	*meters*	*cm.*			*meters*	*cm.*		
1	2.46	2.77	+31	2.58	104.9	2.34	−12	2.29	93.1
2	2.49	2.73	+24	2.54	102.0	2.70[3]	+21	2.65	106.4
3	2.46	2.65	+19	2.46	100.0	2.60[3]	+14	2.55	103.7
Ringling herd									
14	2.16	2.26	+10	2.07	95.8	2.18	+ 2	2.13	98.6
15	2.26	2.49	+23	2.30	101.8	2.34	+ 8	2.29	101.3
16	2.21	2.42	+21	2.23	100.9	2.24	+ 3	2.19	99.1
17	2.11	2.30	+19	2.11	100.0	2.18	+ 7	2.13	100.9
18	2.29	2.43	+14	2.24	97.8	2.34	+ 5	2.29	100.0
19	2.13	2.30	+17	2.11	99.1	2.08	− 5	2.03	95.3
20	2.13	2.31	+18	2.12	99.5	2.24	+11	2.19	102.8
21	2.39	2.62	+23	2.43	101.7	2.70	+31	2.65	110.9
22	2.29	2.47	+18	2.28	99.6	2.24	− 5	2.19	95.6

23	2.18	2.36	+18	2.17	99.5	2.24	+ 6	2.19	100.5
24	2.34	2.59	+25	2.40	102.6	2.44	+10	2.39	102.1
25	2.11	2.31	+20	2.12	100.5	2.04	− 7	1.99	94.3
26	2.24	2.42	+18	2.23	99.6	2.34	+10	2.29	102.2
27	2.36	2.54	+18	2.35	99.6	2.54	+18	2.49	105.5
28	2.36	2.59	+23	2.40	101.7	2.38	+ 2	2.33	98.7
29	2.49	2.75	+26	2.56	102.8	2.48	− 1	2.43	97.6
30	2.16	2.31	+15	2.12	98.1	2.14	− 2	2.09	96.8
31	2.24	2.36	+12	2.17	96.9	2.14	−10	2.09	93.3
32	2.11	2.24	+13	2.05	97.2	2.18	+ 7	2.13	100.9
33	2.44	2.63	+19	2.44	100.0	2.34	−10	2.29	93.9
34	2.31	2.52	+21	2.33	100.9	2.34	+ 3	2.29	99.1
35	2.39	2.54	+15	2.35	98.3	2.38	− 1	2.33	97.5
36	2.29	2.43	+14	2.24	97.8	2.38	+ 9	2.33	101.7
37	2.01	2.20	+19	2.01	100.0	1.98	− 3	1.93	96.0
38	2.13	2.29	+16	2.10	98.6	2.14	+ 1	2.09	98.1
39	2.39	2.59	+20	2.40	100.4	2.48	+ 9	2.43	101.7
40	2.03	2.24	+21	2.05	101.0	2.08	+ 5	2.03	100.0
41	2.03	2.21	+18	2.02	99.5	2.08	+ 5	2.03	100.0
42	2.31	2.48	+17	2.29	99.1	2.24	− 7	2.19	94.8
43	2.44	2.64	+20	2.45	100.4	2.60	+16	2.55	104.5
44	2.26	2.52	+26	2.33	103.1	2.48	+22	2.43	107.5
45	2.34	2.52	+18	2.33	99.6	2.24	−10	2.19	93.6
46	2.34	2.58	+24	2.39	102.1	2.44	+10	2.39	102.1
47	2.31	2.54	+23	2.35	101.7	2.44	+13	2.39	103.5
Average	....	....	+19	....	....	....	+ 5	....	....

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[1] Measured with device illustrated in figure 6.

[2] Measured with elephant's weight on foot.

[3] Left front foot.

Neuffer. The heights of Nos. 5 to 13 are estimated heights furnished us by Trainer Davis, and the heights of Nos. 48 to 63 are estimates furnished by Trainer McClain. According to the data in table 2, thirteen of the sixty-three elephants had heights of 8 feet or over. Of these thirteen, six were measured by us. In addition, the estimated heights of seven of the elephants in the Barnes herd are 8 feet or over. The maximum heights recorded for any of the elephants are that of No. 29, which was actually measured as 8 feet 2 inches (2.49 meters), and that of No. 53, estimated to be 8 feet 4 inches. From all these data it is evident that Jap is in the class of extremely tall female elephants. The reported heights of elephants in zoological parks and many circuses are oftentimes inaccurate and are frequently reported simply to make a "record" of a very tall animal.

The interest in the elephant's height and its practical importance to the elephant man led us to make a more careful study of the two popular methods of measuring these gigantic animals. Having for a basis the actual measurements on elephants Nos. 1 to 3 and Nos. 14 to 47, we made comparable measurements both with the tape thrown over the shoulder and likewise of the circumference of the right front foot. The results are recorded in table 6. The height at the shoulder was determined with the accurate instrument illustrated in figure 6. As can be seen from the fourth column of the table, half the distance over the shoulder from ground to ground is, in all cases, higher than the height at the shoulder. This difference varies in the thirty-seven elephants measured from a minimum of + 10 cm. with No. 14 to a maximum of + 31 cm. with No. 1. The average difference is + 19 cm. If half the measured distance over the shoulder from ground to ground is reduced by 19 cm. to correct for this average deviation, the corrected heights (see the fifth column in table 6) bear a close relationship to the measured heights given in the second column. By this method of comparison the height based on the measurement over the shoulder from ground to ground is from 95.8 to 104.9 per cent of the height at the shoulder. The average deviation is ± 4 per cent. Hence the height of any individual elephant can be measured by the tape method with an accuracy of only ± 4 per cent. The height of an 8-foot elephant can be measured by this method with a maximum error of ± 4 inches, but, as can be seen from the sixth column of table 6, many of the corrected measurements are much closer to the true heights than this. Indeed, nineteen of the thirty-six measurements corrected as outlined above are within ± 1 per cent (*i. e.* about 1 inch) of the true heights.

Although the average correction of + 19 cm. applies to the group of elephants as a whole, inspection of the figures in table 6 shows that for the elephants under 2.25 meters in height the correction would be more nearly + 17 cm., for those from 2.25 to 2.30 meters in height, inclusive, it would be + 19 cm., and for those over 2.3 meters in height + 20.9 cm. Therefore, the general trend is that the taller the animal the larger is the correction to be applied to the height as measured by half the distance over the shoulder from ground to ground.

The value of this type of measurement (which is fairly easily made) is apparent when one compares with the shoulder heights the heights calculated from twice the circumference of the right front foot. (See the last four columns of table 6.) The correction applied when the height is based upon this circumference (disregarding for the moment the inherent error caused according to whether the elephant is resting its weight on the foot or not) is of a very different order of magnitude. Thus the heights as measured by the tape thrown over the shoulder are, in all instances, too high, the average deviation being + 19 cm. (7½ inches). The heights based upon measurements of the circumference of the foot vary from the shoulder height by − 12 cm. in the case of Jap to + 31 cm. in the case of No. 21. In other words, Jap is actually 12 cm. (about 5 inches) taller than the height as indicated by the circumference of her foot and No. 21 is 31 cm. (12 inches) shorter. The average deviation is strikingly small, amounting to but + 5 cm. or about 2 inches. If a reduction of 5 cm. is made in the heights based on the circumference measurements for the individual elephants, the corrected heights to be compared with the shoulder heights are as given in the ninth column of table 6. The results, however, show much higher variations (from 93.1 to 110.9 per cent) from the shoulder height than do the values for the corrected heights based upon half the distance over the shoulder from ground to ground. Thus, although the heights of an *entire group* of elephants can be measured with reasonable accuracy from twice the circumference of the right front foot reduced by 5 cm., the heights of the individual elephants as estimated by this method, may show wide fluctuations from the true heights.

In table 2, page 22, are recorded the estimated heights at the shoulder of the Barnes herd, as given to us by Trainer McClain. Subsequently McClain sent us measurements of the maximum circumference of the right front foot of each of these elephants. Multiplication of these circumferences by two and comparison with the heights at the shoulder, as given in table 2, show that the heights calculated from the circumferences differed from the shoulder heights as follows:

Elephant No.	Calculated height greater or less than shoulder height (inches)	Elephant No.	Calculated height greater or less than shoulder height (inches)
48	+ 6	56	+ 5
49	+ 17	57	+ 2
50	+ 3	58	− 9
51	+ 5	59	+ 2
52	+ 5	60	+ 4
53	− 5.5	61	+ 6
54	− 7	62	+ 7
55	+ 3	63	− 7

Thus under no conditions can one assume that this method of calculation from the foot circumference gives anything but the crudest suggestion as to the probable height of the elephant. Of the two methods of approximating the height, therefore, the one having the less error is that of measuring the distance over the shoulder from ground to ground, dividing by two, and subtracting from this height (in meters) 19 cm.

These two popular methods of measuring the height have been stressed simply to show to elephant men the inherent errors and to show that true shoulder heights only can be accepted as having real value. The simple apparatus described on page 97 makes it easy to measure the true height. There are only two important points to bear in mind, (1) that the cross arm should be precisely at right angles to the vertical rod and (2) that some sort of plumb bob be attached so that the vertical rod will be surely held in a vertical position. Obviously the bottom of the rod should rest on the ground at the same level as the elephant's feet. It is believed from the experience with this device that elephant men who are interested in securing the precise heights of their elephants will find the construction of this simple apparatus inexpensive, and that the results will be highly accurate.

The height, as such, is chiefly of use as a general index of size. It plays no particular rôle in comparisons of the metabolism of animals of various sizes, as such comparisons are usually made upon the basis of body weight or surface area. The important feature of this study of height, however, is that Jap may be considered a very large female and that her height (8 feet 1 inch) compares favorably with most of the largest recorded heights of female elephants. This fact is of interest only in that it shows that our gaseous metabolism studies dealt with one of the largest living terrestrial mammals. Hence, for the particular purpose of comparing the metabolism of the smallest and the largest warm-blooded animals, Jap was practically the largest that we could expect to measure.

Girths and Lengths

Since it was early recognized that the assistance of an engineer was needed in obtaining the linear dimensions of the elephant, only a few measurements of girths were made and these were on Jap alone. Jap appeared rather fat, but elephants in general seem fairly bulky and puffed up. One might infer that this swelling is the result of large intestinal contents, but the findings of Dr. Noback[1] on Kartoum and the data of Gilchrist[2] on the amount of dung in the intestines do not suggest enormous residues in the intestines.

Jap, although unusually tractable in many ways, had either been abused or perhaps was unaccustomed to being handled in this way, so that girth measurements were not easily obtained. Three girths around the belly were measured, one at about the center of the body at the highest part of the body being 4.67 meters. The other two measurements were made around that portion of the body between the hind legs and the high point on the back. Of these the girth nearest the middle of the back was 4.80 meters and the one nearer the hind legs 4.70 meters. The girth around the neck was 2.67 meters and that of the right front leg, just below the first joint (ankle), that is, around the smallest part of the leg just above the foot, was 78.7 cm. For purposes of computing the size of the tube used as a trunk-breathing appliance (Plate 7, page 58), two circumferences, one near the end of the trunk and one about one meter up the trunk, were determined. The first was 36.8 cm. and the second 56.5 cm.

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[1] Noback, C. V., 36th Ann. Report, New York Zool. Soc., 1932, p. 58.

[2] Gilchrist, W., *A practical treatise on the treatment of the diseases of the elephant, camel, and horned cattle, with instructions for preserving their efficiency,* Calcutta, 1851.

A few linear measurements on an "ordinary sized" elephant weighing 4355 pounds (1975 kg.) were reported by W. Gilchrist[1] in 1851. The animal's height was 7 feet 4 inches (224 cm.), its length from the top of the forehead to the insertion of the tail was 10 feet 1 inch (307 cm.), and the girth around the abdomen 13 feet 8 inches (4.17 meters). Sanderson[2] gives the length from the tip of the trunk to the tip of the tail of the largest elephant he ever shot (having a vertical height at the shoulder of 9 feet 7 inches or 2.92 meters) as 26 feet 2½ inches (8.0 meters).

Thanks to the kindness of Dr. Noback, we have been given the privilege of publishing (in table 7) the linear measurements made by him on Kartoum, when 28 years old. (For the weights of the different parts of Kartoum's body determined at the time of autopsy, see table 9, page 112.)

Table 7—*Linear measurements of the male African elephant Kartoum—Noback (October 26, 1931)*

Measurement	Feet and inches		Meters
Height at shoulders (straight line)	10	10	3.30
Height at shoulders when standing (alive)	10	8½	3.26
Over all length (with tape) from end of tail along back to tip of trunk	26	8	8.13
Length of tail	4	10	1.47
Base of tail to front of pelvis (tape)	2	6	.76
Front of pelvis to high point of back (tape)	2		.61
High point of pelvis to low point of back (tape)	2		.61
Low point of back to front of shoulder (tape)	2	6	.76
Front of shoulder to base of skull (tape)	2	6	.76
Base of skull to front of prominence between eyes (tape)	4	7½	1.41
Length of trunk	5	8	1.73
Circumference of trunk at center (variable)	2	5	.74
Circumference of front hoof	4	7½	1.41
Circumference at wrist	3		.91
Circumference half-way between wrist and elbow (2 feet 10 inches up from sole)	3	2½	.98
Circumference of elbow	4	6	1.37
Circumference of smallest place below knee	2	8½	.83
Circumference of knee	4	7	1.40
Width of pelvis	5	3	1.60
Circumference of chest (just behind front legs)	13	4	4.06
Thickness of skin along back		1 to 1¼	2.5 to 3.2 cm.

Body Weight

Although height and the general massiveness, judged by ocular impression, are excellent indices of size, a far more scientific index of size is the body weight. Consequently whatever the interest in the true height of Jap and in the probable error involved in the measurement of her height, there is no question but that an accurate record of her body weight is of importance. Realizing this, we were not content to accept the weights given by her various keepers. From innumerable sources (the keepers, other attendants, and owners) we had been assured that Jap had a weight of essentially 8800 pounds. Since it was necessary to know her exact weight at the time of the metabolism measurements, Jap was taken on March 8, 1935, to the city scales at Campgaw, New Jersey, where the city weigher certified that her weight was 8150 pounds. At this time she was wearing a large canvas blanket, which was subsequently accurately weighed at the barn on the Nutrition Laboratory scales and found to weigh 24.75 kg. The net weight (one single measurement) of Jap was, therefore, 8095 pounds, corresponding to 3672 kg.

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[1] Gilchrist, W., *loc. cit.*

[2] Sanderson, G. P., *Thirteen years among the wild beasts of India*, London, 2d ed., 1879.

However considerable the variations may be in the measurements of height (so far as the point at which the animal is measured, the muscular tonus, and the position of the body are concerned), an equal degree of variability may be expected in the determinations of the body weight of the same animal at different times, not only in the same month or year (even after adult growth has been attained) but also even during the same day. Because of the increase in weight accompanying each ingestion of food and water (which with the elephant may amount to 100 kg. at one time) and because of the loss in weight with each urination and defecation, any single body weight as measured is simply an approximate figure. This point has been especially emphasized in studies with ruminants, where an attempt has been made to use the body weight as an index of equilibrium in feeding experiments. Only a long series of consecutive daily measurements over a period of 14 days is now accepted in our investigations at Durham, New Hampshire, as the best index of the true body weight of steers, cows, and horses. Thanks to the careful supervision of Engineer Ackerman, a series of daily weights was secured on Jap in October 1935, after she had returned to Campgaw, New Jersey, from her summer tour and after she had been at Campgaw for several weeks. Jap was marched a quarter of a mile to the city scales, upon which she had formerly been weighed, and her weights were found to be as follows:

1935	kg.	1935	kg.
October 7	3538	October 15	3593
" 10	3538	" 16	3547
" 11	3547	" 17	3583
" 12	3552	" 18	3593
" 14	3593	" 19	3633

The maximum variation on the ten days of measurement was 95 kg. In four consecutive days, October 16 to October 19, the variation was as great as 86 kg. In consideration of the fact that there was no control of the actual amount of water drunk and food eaten, this variability in body weight is to be expected. These records emphasize that the body weight of the elephant may easily vary 2 per cent within a few days' time. Hence any calculation based upon the body weight alone may have an inherent error of 2 per cent.

A series of body-weight measurements on an elephant was likewise obtained by Schrempp.[1] In his thesis, a copy of which was kindly placed in our hands by Dr. Ludwig Zukowsky of the Hagenbeck Tierpark in Hamburg (Stellingen), Germany, six body weights obtained at weekly intervals are reported for a female Indian elephant, "Matschi," 26 years old, having a maximum height of 2.64 meters. These weights were as follows:

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[1] Schrempp, W., *Betrachtungen über den wilden und den zahmen Elefanten unter besonderer Berücksichtigung der Fütterung und Haltung des letzteren,* Diss., Hannover, 1934, p. 33.

1934	kg.	1934	kg.
May 29	3020	June 19	3012
June 5	3022	June 26	3003
June 12	3020	July 3	3030

Each of these weights was determined between 9 and 10 o'clock in the morning, after the elephant had been fed and given water. The elephant was taken once each day on a tour around the park. Otherwise the activity was the so-called "stall activity." Schrempp points out the difficulty of weighing animals frequently, particularly in zoological parks, which are not often provided with scales of suitable size for such measurements. Furthermore many of the zoological park animals can not be conducted safely to city scales. The extraordinary uniformity in the weights of Schrempp's elephant over a period of six weeks is in striking contrast to the variability noted in the weights of large ruminants and, indeed, the variability noted with Jap. In view of the measurements made on Jap, it is hardly just to assume that the regularity as noted in Schrempp's measurements applies to elephants in general. To what extent the body weight varies due to differences in water intake, in food eaten, and in feces discharged no one knows. From other observations, however, one may conclude that the total contents in the elephant's reservoir for ballast do not change greatly and that the food ingested passes fairly rapidly through the intestinal tract.

Obviously the calculations for Jap in the subsequent pages of this report can be based only upon the single measurement obtained at or about the time of the respiration experiments. The fact that she weighed in October about 70 kg. less than she did in the spring may have been due to the nature of her feeding and to the possible drafts upon body material during the active summer's work. In any event it is believed that there is no justification for making any correction in any subsequent calculations for these weight variations. Hence all our calculations for Jap in the subsequent analysis of her metabolism data (see pages 282 to 289) are based upon the first accurately attested weight of 8095 pounds (3672 kg.).

The same general tendency to exaggerate that one notes in statements with regard to heights of animals is inherent in the showman's claims concerning the weights of his animals. This tendency is unfortunate, because there are only two groups of elephants upon which weight observations can be made, those in zoological parks and those in circuses, and there are difficulties attendant upon weighing these animals. The very large elephants are often shot in the wild and hence are not available for weighing, for there would be no scales in the field even for weighing the individual parts after the body has been dissected. The extremely large animals most frequently deposited in zoological parks are males that have been intractable and dangerous for the circus. They are often too unruly to be moved to suitable scales, and few parks have in their own confines scales for weighing these great animals. Hence their weights have to be estimated, except when autopsies are made, as was the case with the male elephants Kartoum (4710 kg.) and Bolivar (5440 kg.). (See page 108.) Circus animals are weighed only periodically, their weights are not made public, and popular writers have frequently accepted uncritically the statements of the various assistant elephant men with whom they have talked.

In table 2 (page 22) are given the weights and the approximate, estimated ages of the sixty-three elephants studied by us. As will be seen from the second footnote in this table, the actual weights of the thirty-four Ringling elephants were determined for us recently (Nov. and Dec. 1935) through the kindness of keepers Doherty and Davis. For the Barnes herd the weights represent records copied from the notebook of keeper McClain, and for the Downie herd records copied from the notebook of one of the keepers. Of the sixty-three elephants whose weights are recorded in table 2, only seven females exceed the weight of Jap. This shows that Jap is a very heavy female and represents an unusually large elephant.

INTESTINAL CONTENTS OR BALLAST

With a herbivore of the immense size of the elephant the question may properly arise as to whether the amount of active protoplasmic tissue included in the body-weight measurement represents at all the same proportionate amount of the total weight as in the case of the average man or the average dog. Or does the body weight of the elephant include an unduly large proportion of inactive material, such as that in the intestinal contents or ballast? Our interest in this question is not so much because we wish to know the proportion *per se* between the ballast and the total body weight as it is because in our comparative physiological studies we must calculate the heat production of the elephant per unit of body weight and also, in accordance with the time-honored but wholly unscientific custom, per square meter of surface area. From this standpoint the problem is most acute in the case of the ruminant, the body weight of which may include a large percentage of inert intestinal material. At times this inert material has been found to be as high as 40 per cent of the body weight.[1] Rubner [2] early pointed out that the intestinal contents of the rabbit might be as much as 20 per cent of the animal's weight, and Seuffert and Hertel[3] have reported that the stomach contents of the horse represent about 15 per cent of the total live weight. If one is to compare the heat production per unit of weight of an animal whose body weight consists of 20 per cent inert material (ballast) with the heat production per unit of weight of the dog, for example, whose body weight is nearly a net weight (since the intestinal contents are small), a discrepancy would immediately appear, for the body weight of the first animal would be recorded as altogether too large and the heat production per kilogram of body weight would, therefore, be too low. If a net weight without ballast were to be used, then an entirely different picture would be presented.

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[1] Voit, E., Zeitschr. f. Biol., 1930, **90**, p. 259.

[2] Rubner, M., *Die Gesetze des Energieverbrauchs bei der Ernährung,* Leipzig and Vienna, 1902, p. 280.

[3] Seuffert, R. W., and F. Hertel, Zeitschr. f. Biol., 1925, **82**, p. 7.

Precisely those factors that complicate the calculation of the heat production per kilogram of body weight complicate likewise the calculation of the heat production per unit of surface area, for the surface area of the elephant has not been measured. It must be calculated. The best method of calculation is based upon the Vierordt formula $S = K \times w^{\frac{2}{3}}$ in which S equals the surface areas in square centimeters, w the weight in grams, and K a constant factor. This factor has been determined for a great many animals, derived from actual measurements of the surface area and the body weight, and has been found apparently to vary a great deal, for one reason according to whether the body-weight measurement represents the weight with or without ballast. If the ballast represents 40 per cent of the body weight, as has been noted with the steer, obviously the value of K will differ greatly, depending upon which weight is used. Consequently it appears to be a matter of considerable importance to know the probable intestinal contents of an animal, in order to correct the total body weight to net weight. More careful analysis[1] of body surface measurements, however, indicates that this factor for all species of animals lies close to 10, when w is used as the total body weight (in grams) uncorrected for intestinal contents. (Consequently the factor of 10 may be justifiably applied to the total live weight of the elephant in calculating its surface area. (See further discussion on page 283.)

We have been able to find but two records where the intestinal contents of the elephant after death have been carefully removed and weighed. Gilchrist[2] reports a series of measurements on a 4355-pound (1975 kg.) elephant. The feces weighed 261 pounds. The water in the bowels and cavity of the abdomen weighed 270 pounds. Hence 12 per cent of the total body weight was in the form of inert material. According to Noback's measurements the percentage of the body weight represented by the intestinal contents in the case of Kartoum was considerably less than 12 per cent. Thus, at death the total weight of all the various parts of the dissected body of Kartoum weighed 10,390 pounds. The intestinal contents as a whole weighed 745 pounds or 7 per cent of the total weight. The previous history of Gilchrist's animal is not recorded. Kartoum, although apparently in good health up to the moment of death, may easily have been ailing and may not have eaten his full ration, so that this difference between 12 and 7 per cent may be wholly insignificant. In any event, based upon the observations on these two animals, one may conclude that the intestinal contents represent a far smaller proportion of the total body weight in the case of the elephant than has commonly been noted with large ruminants. Hence no attempt has been made to correct the body weight of Jap for intestinal ballast, on the assumption that this (3672 kg.) represents approximately a net weight.

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[1] Benedict, F. G., Asher-Spiro's Ergebnisse d. Physiol., 1934, **36**, p. 300.

[2] Gilchrist, W., *A practical treatise on the treatment of the diseases of the elephant, camel, and horned cattle, with instructions for preserving their efficiency,* Calcutta, 1851.

Autopsies of Elephants

It is not surprising that an animal of the size and configuration of the elephant should have attracted the attention of anatomists at a fairly early date and that on the rare occasions when it has been possible to perform an autopsy advantage has been taken of this. The reports of partial necropsies by Aristotle, Galen, and Moulines have already been mentioned. (See page 7.) Other early reports of autopsies are those by Stukeley[1] in 1715 and 1720, by Camper[2] about 1750, by Pagenstecher[3] in 1872, and by Howe[4] in 1879. There are also brief accounts of an autopsy by Perrier and Phisalix in 1907,[5] by Giard[6] in 1907, and by Mitchell[7] in 1916.

In his autopsy of a 1975-kg. elephant, reported in 1851, Gilchrist[8] made an elaborate series of measurements of the weights of the various parts of the body. Since these data are in a publication that is not easily accessible, they are reprinted in table 8. The length of the small intestine of this elephant was 68 feet (21 meters) and of the large intestine 38 feet 3 inches (12 meters). The depth of the carotid artery from the surface of the neck was 4 inches (10 cm.) and the diameter of the carotid artery ¾ inch.

Reference is made by Miall and Greenwood[9] to the measurements by Owen[10] of a young Indian elephant about 7 feet (2 meters) high at the shoulder (weight not given), which are as follows:

Length of small intestine	38 ft. (11.6 meters)
Total length of colon and rectum together	20 ft. (6.1 meters)
Total length of intestinal canal, exclusive of caecum	58.5 ft. (17.8 meters)

According to Evans[11] the small intestines of four elephants had total lengths, respectively, of 66, 70, 73, and 74 feet (20, 21, 22.3, and 22.6 meters). The total lengths of the large intestines of these same animals were 38, 40, 46, and 43 feet (11.6, 12.2, 14.0, and 13.1 meters).

Autopsy by Fox at Philadelphia, 1908—An extraordinarily complete autopsy was made of a gigantic male, Bolivar, at the Philadelphia Zoological Garden in 1908. This was an Indian elephant, presented to the Philadelphia zoo on December 25, 1888, when about 27 years of age but, like many of the male elephants, he was very ferocious and had killed two men prior to his arrival at Philadelphia. He lived there for twenty years, dying on July 31, 1908. His height at that time was 10 feet at the shoulder. His carcass was cut up, and the various parts were weighed. The total weight

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[1] Stukeley, W., *An essay towards the anatomy of the elephant, from one dissected at Fort St. George, October 1715, and another at London, October 1720,* London, 1723, p. 89. (Reference inaccessible.)

[2] Camper, P., *Description anatomique d'un éléphant mâle, Publiée par son fils,* A. G. Camper, Paris, 1802.

[3] Pagenstecher, H. A., Verhandlungen des naturhistorisch-medizinischer Vereins zu Heidelberg, 1872, **6**, p. 96.

[4] Howe, A. J., Eclect. Med. Journ., Cincin., 1879, **39**, p. 252.

[5] Perrier, E., Compt. Rend., 1907, **144**, p. 236; Phisalix, M., Compt. Rend., 1907, **144**, p. 281.

[6] Giard, A., Compt. Rend., 1907, **144**, pp. 306, 471, and 1318.

[7] Mitchell, P. C., Proc. Zool. Soc. London, 1916, p. 210.

[8] Gilchrist, W., *loc. cit.*

[9] Miall, L. C., and F. Greenwood, Studies in comparative anatomy. No. II. *Anatomy of the Indian elephant,* London, 1878, p. 58.

[10] Owen, R., *On the anatomy of vertebrates,* London, 1868, **3**, p. 457.

[11] Evans, G. H., *Elephants and their diseases,* Rangoon, 1901 and 1910.

TABLE 8—*Weights of dissected organs and body parts of elephant—Gilchrist (1851)*

Organ or part	Weight	
	Pounds	Kilograms
Head (including brain, which weighed 16.5 lb.)	470	213.2
Left fore-leg	305	138.3
Right fore-leg	294	133.4
Left shoulder	102	46.3
Right shoulder	119	54.0
Left hind-leg	291	132.0
Right hind-leg	308	139.7
Left ribs	160.5	72.8
Right ribs	250	113.4
Loins and part of buttock	352	159.7
Pelvis	383.5	174.0
Neck	97	44.0
Breast-bone	84	38.1
Heart	42	19.1
Lungs and diaphragm	98	44.4
Kidney	16	7.3
Intestines (small and large bowel)	275	124.7
Liver	76.5	34.7
Spleen	4.5	2.0
Stomach	96	43.5
Total weight of carcass and organs	3824	1734.6
Dung	261	118.4
Water in bowels and cavity of abdomen, about	270	122.4
Total weight	4355	1975.4

was 12,000 pounds (5440 kg.). No organs were weighed except the heart. Dr. Herbert Fox, Curator of the Research Laboratory, performed the autopsy. The results have not been published except in extremely condensed form in the annual report of the Philadelphia Zoological Garden for 1909. We are very grateful to the Director of this Garden, Dr. Roderick Macdonald, for the privilege to report here the full details, which are as follows:

AUTOPSY OF THE ELEPHANT BOLIVAR, BY DR. HERBERT FOX

Indian Elephant (*Elephas indicus*) Habitat—India, Ceylon, etc.
Received December 25, 1888—Died July 31, 1908. Adult Male.

Clinical Notes: Has been rheumatic and losing flesh, but there were no special symptoms before 6 a. m. this morning, when he was found down and unable to get up.

Pathological Diagnosis: Chronic polyarthritis
Chronic myocarditis
Parenchymatous nephritis
Chronic tuberculosis of the lungs partly encapsulated
Pigmentation of the spleen

Autopsy Notes

The pleuræ are not fat, but the surfaces are smooth and devoid of adhesions. The lymph nodes of the mediastinum are about 10 x 20 cm. for the largest; the small ones vary around 2 x 4 cm. They are firm, deep red-brown, without clear divisions into medulla and follicular cortex. There are several large, firm, pale, rather cheesy follicles in all the large ones and a few of the small. These do not appear like tuberculosis.

The lungs are flaccid and soft; gray and red mottled. The bronchi are firm and stand open. Around one in the upper lobe of the right lung, there is a large area of cheesy degeneration, around which a zone of connective tissue has formed. This extends about the bronchus in a sheath-like manner. There is also a separate nodule the size of a cherry, with a cheesy center. The trachea appears normal. The mucous membrane is soft and pale pink. No excess of mucus. Tubercle bacilli could be demonstrated in the cheesy nodules.

The heart weighs 42 pounds (19.1 kg.). It is 56 x 32 cm., empty. The wall of the left ventricle varies in thickness from 6 to 8 cm. and that of the right ventricle, 1.5 to 2 cm. The muscle is firm in consistency and normal in color. The peri-, epi-, and endocardia are pale, smooth, and transparent. The valves are normal. The mitral is slightly rough on its superior surface, but smooth and soft elsewhere. The valves are all apparently competent. The aorta is smooth, pale yellow, and normally resilient. 10 cm. above the valves it measures 2.5 cm. The pulmonary artery measures 2 cm. at the same place. There are three areas of thickening, with a pale fibrous zone around them in the sinus around the opening of the anterior coronary artery, proximal to the semilunar fold of the wall at the origin of the left lateral branch.

The peritoneal surfaces of the abdominal viscera examined are smooth.

The liver is smooth, firm, tough; when cut, preserves these characteristics. The vessels are empty. The surface presents an obscure nutmeg appearance. The interstices contain rather an abundance of connective tissue, but there seems to be no destruction of tissue or loss of topography of the lobules.

The spleen is covered by a thick gray and yellow capsule 2 mm. thick. The section shows a greenish brown, fibrous organ. There are no visible follicles. The pulp is very firm.

The kidney is made of ten lobes well developed, each with its own medulla and primary pelvis, which opens into a large common pelvis. The medulla is narrow and the striæ are marked. The cortex is wide. The medullary rays are not easily distinguishable, but there are many pale striæ running from the medulla and becoming more regular and finer as they proceed outward. They are irregular near the medulla, and the part of the cortex between is also irregular. In some parts of the organs the glomeruli are quite plain in this region and also near the margins of the lobe. The capsule comes off with some difficulty, but does not tear the surface. It is fine and pale.

The adrenals are firm and gray and yellow on the surface. The medulla is dull gray and the cortex dull tawny brown. It is apparently divided into rectangular lobules without definite walls.

The rest of the viscera were thrown away.

The parathyroids were found and were probably the superior and middle pair. They were about 3 x 5 cm. and 2 x 2.5 cm. Dense, deep, red-brown, firm, congested, with very little structure except fine, distinct, connective tissue septa.

The joints were swollen, for the most part, and in the right, hind, second joint there was an especially large accumulation. The tip end of the right femur was ulcerated at the edge where the cartilage joins the bone. In all the carpal and tarsal joints and the articulations of these with the phalanges, the cartilages are irregular and hard. There are evidences of long standing arthritis in every joint. There are no calcareous deposits.

Histological Notes

Lungs—Around the cheesy area mentioned in the notes there is a low grade, chronic granulation tissue, in some places enclosing cheesy masses with giant cells on the margin. The neighboring septa are slightly thickened and in some places broken, forming emphysematous cavities (some of these cavities are edematous).

Heart—The most striking thing is the irregularity of the nuclei. Some are narrow and compact, whereas others are pale and granular. Most of them lie in large spaces, some of them are surrounded by blood, whole or disintegrated. The markings of the muscle are obscure, in some places entirely missing. Here and there one sees a distinct hyaline degeneration of the muscle. At some places there is edematous distension of the perinuclear spaces, which seems to encroach upon the muscle cell structures. Almost all the nuclei have pigment at the poles. The whole organ is beset in an irregular manner with fibroblasts, plasma cells, and a few lymphocytes. The tissue about the blood-vessels is edematous and rich in fibroblasts. Nothing like an Aschoff body is visible.

Liver—The interlobular ramifications of the capsule are very prominent. They consist of pale hyaline areas, poor in cells, most of which are fibroblasts. This connective tissue increase has distorted and cut off some lobules. The columns of liver cells are rather distorted but maintain their general relations. The cells are laden with pale, coarse, granular pigment, slightly in excess of what would seem normal. (Elephant liver cells are normally multinuclear and contain pigment.) There is no increase of the bile ducts. The intercellular capillaries contain large quantities of cellular detritus and pigment.

Spleen—The pulp is overladen with coarse, golden brown pigment and the large pale septa poor in cells but most being fibroblasts dominate the picture. Follicles are few in number, loosely arranged, and contain a goodly number of pulp cells (splenocyte type).

Parathyroid—Shows marked congestion in a sinus arrangement, but the parenchyma shows no distinct architecture. This deserves future study.

Adrenal—Negative.

Kidney—Medulla and medullary rays show edema with the presence of some fibroblasts. The parenchyma shows a rather depressed condition of epithelium such as is seen in chronic parenchymatous nephritis. In the tubules are plugs of detritus, some quite small, others amounting to coarse, granular casts. Some few of the cells are without nuclei. The glomeruli are large, and the tuft seems normal. It fills out the capsular space. The capsule is several times as thick as the human. It is slightly irregular. The epithelium is not visible at all places. Many fibroblasts may be seen in various capsules.

In 1935 Dr. Fox examined the skeleton of Bolivar at the Academy of Natural Sciences in Philadelphia and kindly sent us the following notes:

"The epiphyseal ends of the bones all over the body show an abnormal porosity. This is more developed around the ends of the bones and not evident on the direct articulating surface. The edges of the ilium and scapula are especially rough, and the condyles of the mandibles are uneven. The epiphyseal borders of the metatarsal bones are unusually rough. The articulating surfaces are in some places very smooth as if eburnated, other places ridged and ribbed as if the cartilage had been damaged at that point. Vertebræ show ventral productive osteitis 4th and 5th, 9th and 10th, 18th and 19th). The osteophytes of the 9th and 10th are approaching each other as if ankylosis were about to be produced. The articulating surface of the right humero-ulnar joint appears to be most eroded. Changes in the left humero-ulnar joint approach the changes in the right."

TABLE 9—*Weights of dissected organs and body parts of male African elephant Kartoum—Noback (October 28, 1931)*

Organ or part	Weight	
	Pounds	Kilograms
Liver	93	42.2
Blood, small part	105	47.6
Head skull (roughened out)	577	261.7
Lower jaw	115	52.2
Heart	50	22.7
Lungs (including muscle and other tissue)	348	157.9
Stomach, intestines, etc. (washed out), empty	486	220.4
Hide, whole	1345	610.1
Trunk musculature	153	69.4
Muscle (loose)	3641	1651.6
Bones (roughened out), not all	1341.5	608.5
Front and hind legs, right	1326	601.4
Right testicle	3.5	1.6
Left testicle	4	1.8
Right kidney	8	3.6
Left kidney	9	4.1
	9605	4356.8
Intestinal contents	745	337.9
Spleen	40	18.1
Total weight	10390	4712.8

Autopsy by Noback at New York, 1931—Another gigantic male, Kartoum, an African elephant, died at the New York Zoological Park on October 26, 1931, when 28 years old and weighing 4710 kg. Dr. C. V. Noback made careful weighings of various parts of the body and an extensive series of length and girth measurements. Only an abbreviated report of this important study has thus far been published,[1] and we have been privileged by the Director, Dr. W. Reid Blair, and by Dr. Noback to report the details. The measurements of lengths and girths have already been cited on page 103, table 7. The weights of the dissected organs and body parts are given in table 9. Dr. Noback states that after a careful washing out of the digestive tract, no macroscopic parasites were found in Kartoum.

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[1] Thirty-sixth Annual Report, New York Zool. Soc., 1932, p. 58.

Probably no one man has autopsied any more elephants than has Professor T. Wingate Todd of Western Reserve University, Cleveland, Ohio. Unfortunately these autopsies were made for only specific purposes and were not general. Hence no data comparable to those on Bolivar and Kartoum are available. We have enjoyed, however, the advice of Professor Todd on a number of occasions in the preparation of this manuscript, and we are very grateful for it.

Autopsy of heart of Mollie at Franklin Park—On March 21, 1921, a female Indian elephant, Mollie (said to be 40 years old), died at Franklin Park, Boston. Observations on the heart were made by Dr. P. D. White of the Massachusetts General Hospital, Boston, and Dr. C. S. Burwell, now Dean of the Harvard Medical School. A full report of the cardiac findings is soon to be made by Drs. White, Burwell, and King, the latter of Seattle, who has recently also dissected an elephant's heart. Dr. White states that Mollie's heart was perfectly normal and weighed 42½ pounds (19.3 kg.). Mr. D. J. Harkins, Curator of the Zoological Garden at Franklin Park, states that the Park records show that Mollie was weighed on the Franklin Park yard scales on June 6, 1920, when her weight was 8180 pounds (3710 kg.). Mr. Harkins reports that when Mollie was dying she "fell and was unable to regain her feet, and thrashed on the floor from 5 a. m. to 10 a. m. This was the third seizure of this kind the elephant had in about as many years." Her carcass was cut up piecemeal by employees of a rendering plant and hauled to their plant in Boston, but no attempt was made to weigh the carcass. Mollie has been credited with having given birth to a young one, but Harkins states that his records show that she never at any time produced young.

These autopsies here reported are the most complete that we have been able to find. Other obscure or inaccessible references regarding partial dissections have been found occasionally. These cited here are mentioned on account of their completeness, and the data are used in subsequent discussions in this text. That more autopsies on elephants have not been made is perhaps explained by the fact that, for the most part, the elephant is shot in the wild and it is difficult to transport the body to a place where a suitable dissection can be made. This technique would be in the nature of an engineering feat. Elephants are rarely killed in zoological gardens or circuses, and when they die in captivity usually only incomplete studies are made. The fact that the skeleton may be demanded for mounting in one museum and the stuffed skin in another frequently leads to divided interests in the disposal of the dead animal, so that suitably adequate anatomical studies are rarely made.

Body Composition

From the physical and chemical standpoints more particular evidence as to the chemical composition of the bodies of these huge animals is desirable. Nothing in the external appearance of the elephant places it in the category of excessively fat animals, such as the sea-elephant, the walrus, and the hog. Yet the elephant does not give the impression of having a low fat content. Too little is known regarding the chemical composition of the elephant's body, its gross make-up, and its percentage of fat, although the literature suggests that the elephant does not fatten as readily as does, for example, the beef steer. In the final comparison of the vital activities of the elephant, particularly the metabolism, with those of other animals it will be important to know whether or not the weight of the elephant is made up in large part of metabolically inert, fatty tissue. In none of the autopsies of elephants reported in the literature is there any comment by the investigators concerning excessive amounts of fat. A second factor tending toward the idea that the elephant's body is not made up of an undue proportion of fat is the fact that these animals are fed by man and present a real economic problem. Hence many of them, especially in the smaller circuses, have to do considerable amounts of work, and excess fat would be disadvantageous. Furthermore, the cost of feeding animals for fattening is great, and both menageries and circuses would be disinclined to overfeed their animals. Indeed, there is a tendency, especially during the winter season, to feed them in general on low rations. We believe that Jap was by no means overfed, and all the evidence we could gather suggests that she probably went through the winter on scant rations. It is obvious, however, from the external appearance of Jap as shown by the photograph taken of her (fig. 1) and as shown by the measurements of her weight and girths, that she was by no means emaciated at the time of our study. In fact, she looked plump, well filled out, and in excellent condition, measuring up well with the better animals of the splendid Ringling and Barnes herds.

RESPIRATION RATE

One of the factors closely associated with the intensity of vital processes is the respiration rate, for excitement or physical activity is almost invariably accompanied by an increase in respiration rate. With these large animals respiration rates have been rarely recorded. Thus, in the literature we are able to find only the statement of Evans[1] that the rate is from 12 to 16 per minute.

Brody's experiments—In his brief report of his experiments on four elephants, Brody[2] does not mention the respiration rate. Through his courtesy, however, in placing all his protocols at our disposal, we are privileged to make use of his unpublished records, and since these include spirometer tracings obtained with a closed-circuit respiration apparatus (see page 57), the respiration rates can be calculated therefrom. Irrespective of whether or not there can be complete collection of respiratory gases from the trunk of the elephant by the closed-circuit method, there is no question but what these graphic tracings give a true picture of the respiration rate. From these tracings have been counted the respiration rates, which are recorded in table 10. The elephants, save in one instance (the second record with No. 52, when she was lying), were in the standing position and in

[1] Evans, G. H., ***Elephants and their diseases***, Rangoon, 1901 and 1910.

[2] Brody, S., Procter, R. C., and U. S. Ashworth, Univ. Missouri, Agric. Expt. Sta., Research Bull. 220, 1934.

all cases awake. The first record on elephant No. 1 was obtained at 11 a. m. All the others were secured between 5 and 6 p. m. Each line in the table represents data from an experimental period of about six minutes' duration. The average respiration rate, based upon all the records except that obtained when elephant No. 52 was lying, is 8.2 per minute. The single observation on No. 52 when lying showed a rate of 5.7 per minute. These spirometer records, which lack of space unfortunately prevents publishing, show some especially interesting features of the character of the elephant's respiration, although obviously one might expect the strange condition of a mask placed over the trunk to result in slightly abnormal respiratory activity. With elephant No. 52 when in the lying position there was definite apnœa at the end of each respiration. The breath was held at the end of each respiration practically the equivalent of the entire time representing the inspiratory and expiratory phase. This phenomenon was shown in less degree when No. 52 was standing, and occasionally by one of the other elephants (Nemo), but usually the expiration followed almost instantly at the end of inspiration. Certain details of the respiratory activity as shown in table 10, such as the volume of inspiration and the average volume of air exhaled from the lungs, will be discussed later. (See page 121.)

Table 10—*Respiration rates and ventilation of lungs of the elephants*[1] *studied by Brody*

Elephant No.	Sex	Age	Weight	Date of measurement	Respiration rate	Volume of one expiration		Average volume exhaled by lungs per minute (as measured)
						Maximum	Average	
		yrs.	*kg.*			*liters*	*liters*	*liters*
Jap, No. 1	F	40	3630	Aug. 30, 1932	8.8	46.4	26.5	233.2
" " "	"	"	"	" " "	11.8	62.4	35.2	415.4
Nemo	M	10	1360	Aug. 30, 1932	6.6	43.1	19.9	131.3
52	F	40	4127	Aug. 4, 1933	7.8	65.7	39.8	310.4
"	"	"	"	" " "	5.7[1]	66.3[1]	39.8[1]	226.9[1]
51	F	35	3743	Aug. 4, 1933	8.0	66.3	46.4	371.2
"	"	"	"	" " "	7.5	68.3	40.5	303.8
"	"	"	"	" " "	7.0	56.4	46.4	324.8

[1] Each line of data represents one experimental period of about 6 minutes' duration; elephants were standing in all instances, except second record with No. 52, when she was lying; all were awake.

RESPIRATION RATE OF THE ELEPHANT JAP

Several methods of studying the elephant's respiration rate were available to us, and our records are the resultant of the use of these methods. Thus, with each expiratory blast of the elephant one could feel the air discharged from the end of the trunk, either against the face or against the hand. At night, when everything was quiet and the elephant was sleeping, the respirations could be easily heard, as the noise of breathing was at times marked. In the trunk-breathing experiments the excursions of the bell of the spirometer, which connected directly with the elephant's trunk, could be easily seen and counted. An assistant watched the spirometer bell and counted the number of its upward movements (indicating the expiratory blasts of the animal) throughout the seven to nine minutes of the experiment. A stopwatch was used to note the exact time. A few observations, based on these three methods, were made on Jap in both series of tests.

Respiration rate when standing—When Jap was standing, with her trunk in almost incessant motion, it was practically impossible to count accurately the respirations per minute, and this difficulty was augmented by the noise and confusion outside the barn. Consequently few accurate measurements of the respiration rate of Jap while standing and awake were obtained. In the respiration experiments in which the end of Jap's trunk was inserted in a tube, the number of respirations during the entire period of each metabolism measurement was counted in three instances. This was on March 17, in the forenoon. The first count was 76 respirations in seven minutes, the rate per minute equalling 10.9 respirations. The second count was 86 respirations in 9 minutes or 9.6 respirations per minute, and the third count was 79 respirations in 8.19 minutes or 9.6 respirations per minute. These records were not so accurate as graphic tracings of the excursions of the spirometer bell in a closed-circuit apparatus would have been, but the results suggest a high degree of accuracy. The data on Jap from the breathing apparatus are of value in showing the respiration rate of the animal when awake and standing, although perhaps complicated by the fact that the breathing appliance was in use. On the assumption that the attachment of the respiratory valve system did not alter the type of respiration, it can be maintained that for this particular animal the average respiration rate, while standing and awake, is approximately 10 per minute.

Respiration rate when lying asleep—In the second Campgaw expedition special emphasis was laid upon studying the respiration rate of Jap when lying, and on several nights between April 5 and 11 counts were made on Jap while she was lying asleep. These counts indicated the following respiration rates:

	Respirations per minute
Apr. 6 (asleep)	4 to 4.5
Apr. 7, 2.08 a.m.	4.5, 4.8, 4.8, 4.4, 4.6, 4.5, 4.9
Apr. 7, 3.00 a.m.	6.2, 6.2, 6.3
Apr. 8, 1.30 a.m.–2.23 a.m.	4.1, 4.5, 5.0, 4.5, 6.0, 7.3
Apr. 8, 2.43 a.m.–2.51 a.m.	3.9, 5.3
Apr. 9, 3.23 a.m.–4.00 a.m.	4.5, 4.9, 4.5, 4.5, 4.4, 5.0, 4.5, 3.8, 4.6, 4.4, 4.4
Apr. 11, 3.05 a.m.	3.8, 3.8, 3.6, 3.6, 3.8, 3.6, 4.0, 3.8, 3.6, 3.5, 3.7, 3.7, 3.6, 3.6, 3.5

Respiration rate when standing and awake—Efforts were made several times to note the respiration rate while Jap was standing quietly, but usually the results were uncertain. When the trunk-breathing experiments were made, her respiration rate, according to the spirometer tracings, was 10 per minute. After these observations were completed, we found that one of the elephants studied by Brody happened to be Jap. Hence the first two respiration rates given in table 10 represent data obtained on the same animal studied by us. Our spirometer records showing a rate of 10 respirations per minute for Jap are in fair agreement with the two rather widely diverging values of 8.8 and 11.8 derived from Brody's curves. If the rate of 10 per minute noted from our spirometer tracings is accepted as correct, the inference is that Jap's respiration rate while lying and asleep was almost half that while she was standing and awake. The lowest individual count noted with Jap was 3 per minute. The profound decrease in metabolism due to sleep, which has been found with so many humans to be not far from 10 per cent, unfortunately could not be studied with the elephant. The decrease in Jap's respiration rate with change from the standing to the lying position and sleep amounts to about 50 per cent.

Respiration rate when standing and asleep—The general impression that the elephant sleeps while standing or more probably dozes while standing is borne out by the respiration rate as counted in a number of instances with Jap when she was standing quietly at night, without external noise. Thus, on the night of April 7 at about 5 a.m., while Jap was standing apparently dozing or asleep and her trunk was still enough to record accurately the expiratory blasts, seven separate counts indicated a respiration rate of 3.9 per minute. This rate is actually lower than the records obtained two hours earlier that night when she was lying. One noticeable characteristic observed with Jap was that when she was standing and asleep the respiratory movement resulted in a slight vibration of the finger of the trunk, whereas when she was lying and asleep the end of the trunk remained without motion and even the small finger did not move. So incessantly in motion is the end of the elephant's trunk that on those rare occasions when the end is resting on the floor and not in movement one may be certain that the animal is dozing while standing, if not actually asleep. This characteristic of sleeping while standing is true of the horse as well as the elephant. The peculiar anatomical structure of the horse's legs, particularly the hind legs (a minimum exertion of which is required to maintain the horse in the standing position), has been frequently commented upon. Study has shown that the action currents of the muscles of the horse's legs are very much reduced or entirely absent. It is clear that an anatomical study of the action currents in the muscles of the legs of the elephant would be most interesting.

Respiration Rates as Studied on Two Herds of Elephants

Three further studies of the respiration rate were made on different occasions: (1) A short series of observations of only a fragmentary character on the Ringling herd one night at the Boston Garden; (2) a series of observations on a number of the Barnes herd of elephants when lying down in the late afternoon on August 1; and (3) an extended study of the elephants of the Ringling herd in their winter quarters at Sarasota, Florida. The most striking feature of the Boston Garden study of the Ringling herd was that these animals gave evidence of being in profound slumber almost immediately after lying down. In several instances two minutes after their heads struck the floor one could count respiration rates of about 4 or 5 per minute, accompanied by loud breathing or snoring.

BARNES HERD

With the Barnes herd, the working herd, in the late afternoon of August 1, ten of the eighteen animals were seen at various times lying down. Apparently they were asleep. This, however, is not certain. One observation only was made on each elephant, this observation lasting from half a minute to a minute. Hence the counts were not so precise nor so extended as with Jap and the Ringling elephants studied at Sarasota. The Barnes elephants showed the following rates during the time that they were studied, all the values being obtained while they were lying down:

Elephant No.	48	52	53	54	56	58	59	60	61	62	63
Respirations per minute	5.8	7.6	6	7.5	5	10	5.5	6.1	6.5	9.6	6.7

These fragmentary and superficially determined values ranged from 5 to 10, and the average for the entire herd was 6.9. Three of these elephants (Nos. 58, 59, and 61), with which rates of 10, 6.5, and 5.5 were found, were recorded as "apparently asleep."

Incidentally, it transpires that two of the other elephants studied by Brody, Nos. 51 and 52, were those upon which fragmentary observations on other physiological factors (not including the gaseous metabolism) were subsequently made by us when studying the Barnes herd at St. Stephen, New Brunswick. With one of them, No. 52, the respiration rate was counted once while she was lying down at St. Stephen. Eight respirations were counted in 63 seconds, corresponding to 7.6 per minute. This is somewhat higher than the rate of 5.7 per minute counted from Brody's curve.

With the Barnes herd, as with all the other elephants, repeated efforts were made to determine the respiration rate while the animals were standing, but the incessant movements of the trunk and the difficulty of noting the expansion of the abdomen during inspiration made it impossible to secure accurate records. So far as it is possible to judge from ocular observation, however, those rates thus estimated for the Barnes herd were not far from the rates noted by us in the case of Jap in the trunk-breathing experiments when spirometer tracings were secured, and the rates noted by Brody with his spirometer. From our series of observations on Jap, Brody's series on Jap, and those on the Barnes herd, it is clear that the respiration rate of the elephant while lying quietly may be as low as 4 or 5 per minute, and while standing awake not far from 10 per minute.

STUDY OF RINGLING HERD IN FLORIDA

The differences noted in the respiration rates of these various elephants and the fact that the observations on the Barnes herd were altogether too short and too few justified further study of the Ringling herd. It was hoped to secure observations while they were standing and awake, but the incessant movement of the trunk ruled this out, as in the other cases of attempted measurement. However, many of these elephants lay down at night and were either profoundly sound asleep or at least quiet. The respirations of these animals, therefore, were readily counted by noting the noise of the discharge of air from the end of the trunk. With twenty-four of the thirty-four elephants records during lying (when some of them were probably really asleep) were obtained.

With two of the animals (Nos. 42 and 35), the times for eleven and thirteen successive respirations, respectively, were recorded with a stop-watch graduated in hundredths of a minute. Thus a hint was secured as to the irregularity in the time between the ends of expirations. The respiration rates given in table 11 were calculated from the number of counts and the time occupied. Since there was a cumulative counting and a cumulative time, the average respiration rate of each elephant would be best represented by the last record, namely, eleven counts in 3.03 minutes in the case of No. 42 and thirteen counts in 2.03 minutes in the case of No. 35.

Table 11—*Respiration rates of two elephants (lying), calculated from the times for successive respirations*

Elephant No. 42			Elephant No. 35		
Number of counts	Time	Respirations per minute	Number of counts	Time	Respirations per minute
	min.			*min.*	
1	0.31	3.2	1	0.22	4.5
2	.52	3.8	2	.44	4.5
3	.80	3.8	3	.59	5.1
4	1.02	3.9	4	.73	5.5
5	1.37	3.6	5	.89	5.6
6	1.55	3.9	6	1.00	6.0
7	1.89	3.7	7	1.13	6.2
8	2.17	3.7	8	1.28	6.3
9	2.50	3.6	9	1.46	6.2
10	2.79	3.6	10	1.61	6.2
11	3.03	3.6	11	1.78	6.2
			12	1.91	6.3
			13	2.03	6.4

The observations on No. 42 show great regularity, varying only from 3.2 to 3.9 per minute, with an average of 3.7. With No. 35 much irregularity is noted, with rates inside of a period lasting but 2.03 minutes varying from 4.5 to 6.4 per minute and averaging about 6 per minute. On the other hand, the last seven counts with No. 35 took place in 1.03 minutes, giving a rate of essentially 6 per minute.

The complete records for the Ringling elephants that were lying are given in table 12. Practically all the observations were made between 10 p.m. and 5.42 a.m., with the greater number made after midnight. According to the data in table 12, the average respiration rate of these elephants when lying, not necessarily asleep, is 5 per minute. No. 33 had a respiration rate of 2.9. This animal likewise had next to the lowest heart rate of any of the elephants we studied. (See table 14, page 133.) The next lowest average respiration rate was that of No. 42, namely, 3.6. The highest of all was that of No. 19, a definite count of 25 respirations in 3 minutes indicating a rate of 8.3 per minute. The general average for the entire herd was 4.9 respirations per minute. This is measurably lower than the average of 6.9 found with the Barnes herd while they were lying down in the afternoon, but the counts with this latter herd were altogether too few for perfect averaging. The average value for Jap was 4.5, although on the last day (April 11) her rate averaged 3.7. Therefore, Jap was in conformity with most of the Ringling elephants, having a respiration rate when lying quietly of not far from 4 or 5 per minute.

Table 12—*Respiration rates of Ringling elephants (lying)*

Elephant No.	Rate per minute	Average rate
14	5.1, 5.5	5.3
16	5.0	5.0
17	4.2	4.2
18	5.1, 5.0, 4.4	4.8
19	8.3	8.3
20	5.6, 5.2, 5.1	5.3
21	5.2, 4.4	4.8
22	5.6	5.6
23	4.1	4.1
24	4.3, 4.2	4.3
27	5.3	5.3
28	5.5, 4.1	4.8
29	4.3	4.3
33	2.9, 2.8	2.9
34	5.7	5.7
35	6.4, 4.5, 4.5, 5.1, 5.5, 5.6, 6.0, 6.2, 6.3, 6.2, 6.2, 6.2, 6.3, 6.4, 5.6, 6.1	5.8
37	4.7	4.7
38	6.5, 5.0, 5.4, 5.5	5.6
39	3.9, 4.9	4.4
40	4.7	4.7
41	5.3, 4.7	5.0
42	3.8, 2.9, 3.2, 3.8, 3.8, 3.9, 3.6, 3.9, 3.7, 3.7, 3.6, 3.6, 3.6	3.6
43	4.0, 4.0, 3.8	3.9
46	6.0	6.0
Average		4.9

Evans's reported respiration rate of 12 to 16 per minute is notably higher than any of the rates recorded by us, although our observations on the standing elephant are very few. This comparison suggests that the observations reported by Evans both of respiration rate and heart rate (normal rate given by Evans as 46 to 50) were not made on tranquil elephants.

VENTILATION OF LUNGS

Although in the trunk-breathing experiments with Jap no tracings were obtained of the excursions of the spirometer bell, since the open circuit was used, nevertheless ocular observation indicated that the elevation of the bell with each expiration varied considerably. This variability was far greater than was shown by the spirometer tracings obtained with Brody's elephants, with which the regularity of respiration was for the most part striking. In an orientation test with Jap on March 16 several observations of the volume of maximum expiration were made. When the spirometer bell was at its lowest level, the blower was stopped. There would then be a small expiration by the elephant, which would raise the bell slightly, then another expiration, and finally a very deep expiration. Following this deep expiration the blower was started, the air removed from the bell, and the experiment repeated. By this procedure it was found that the maximum expirations raised the spirometer bell 26 cm., corresponding to 36 liters.

Several times on March 16 Jap gave premonitory symptoms of being ready to sneeze. This may have been due to her having sucked into the trunk some irritating substances from the floor or she may have had an incipient cold. On these occasions the volume of expired air (not measured by the spirometer) appeared to be literally enormous. The impression as to the volume of these blasts, however, was probably greatly influenced by the noise that Jap made. It was a noise characteristic of sneezing, and the volume of air expired under such conditions can not be considered as an accurate measure of the total volume of air leaving the end of the proboscis.

The apparent ventilation of the lungs, as indicated by the measurement of the volume of air passing through the meter per minute during the trunk-breathing experiments with Jap, was 209, 209, and 232 liters (reduced to standard conditions of temperature and pressure).

From the spirometer tracings and the factor of his spirometer bell as sent to us by Brody, we have calculated the maximum volume of one expiration, the average volume of one expiration, and the average volume exhaled per minute. These are recorded in table 10, page 115, along with the data on the respiration rate per minute. Since three of the animals, Jap, No. 51, and No. 52, were essentially of the same size and weight, the differences in lung ventilation are not significantly striking. It is worthy of note, however, that the very low ventilation rate per minute noted with Jap of 233 liters is in exactly that period when the low metabolism was measured. On the other hand, the low ventilation rate for No. 52 occurred during a period of lying down. Nemo, with a ventilation rate of 131 liters, weighed only about one-third of the other three.

These results in table 10 and the ventilation rates noted by us with Jap are based on respiration experiments made with the trunk only. As will be explained subsequently (page 267) when the chamber respiration experiments are compared with the trunk-breathing experiments on Jap, probably about 30 per cent of the air entering into the respiratory processes is not discharged through the trunk. Hence the lung ventilation as measured both by Brody's technique and by ours should be increased in the ratio of 70 : 100. Thus the average ventilation rate as measured in the three trunk-breathing experiments with Jap, 217 liters, should be increased to 310 liters to represent more nearly the true lung ventilation, and Jap's maximum volume of expiration, instead of being 36 liters, should be about 50 liters.

HEART RATE

The close correlation between the heart rate and the metabolism noted with many humans has resulted in added interest in the heart rate when associated with metabolism experiments in comparative physiological studies. The fact that there is so little information in the early literature regarding the heart rate of the elephant emphasizes the difficulty of determining the heart rate of an animal of this size and with such a tremendously thick skin. As early as 1851 Gilchrist[1] commented that "49 is the average healthy pulsation of the heart" and pointed out that it may increase (by exercise, it is presumed) to from 90 to 100 beats per minute. Gilchrist also emphasized that the best place for counting the heart rate is at the back and root of the ears. He states that the elephant may become excited when being approached by a stranger and will rarely remain lying down and sufficiently quiet for the required time, and that the best way is to have the mahout count aloud the pulsations while the elephant is standing and "when the circulatory system is not disturbed by fear or exertion on the part of the animal." Colin,[2] without describing the technique employed, states that "according to his observations" the heart rate of the elephant (probable weight, 2000 kg.) is from 25 to 28 beats per minute.

In Evans's book,[3] published in 1910, considerable discussion is given regarding the method of obtaining the heart rate by noting the pulsations of an artery at the back and root of the ear. "If the finger be applied to an artery, the vessel will be found to expand between 46 to 50 times a minute." Evans restates the suggestion of Gilchrist to have a mahout trained to call out each pulsation and an observer to time it.

In 1918 Pütter,[4] in one of his series of articles on comparative physiology, calculated the heart rate of an elephant at rest, weighing 3000 kg., as 23.4 beats per minute and the heart rate of an elephant at rest, weighing 3500 kg., as 22.2 beats. He also states that actual records were obtained showing rates of 22 to 28 beats. No hint is given as to where or how these records were obtained.[5] In the text Pütter refers to the "pulse rate" of the elephant as 22 to 26 beats and, indeed, 28 beats per minute. This article by Pütter contains interesting, although at times fantastic but stimulating, conceptions. In this particular paper he is dealing with the relationship between the pulse rate during rest and activity and the body weights of various animals, ranging from a dwarf bat weighing 3.73 gm. to a whale calculated to weigh 265,000 kg.

Alexander Forbes and his associates[6] obtained an electrocardiogram from an elephant (weight not given), from which they have calculated the heart rate, although their particular interest was in the form of the wave rather than in the heart rate per minute. They report that the times for nine successive beats were, on the average, 1.46 seconds per beat and that the average heart rate (elephant standing) was 41 per minute.

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[1] Gilchrist, W., *A practical treatise on the treatment of the diseases of the elephant, camel, and horned cattle, with instructions for preserving their efficiency,* Calcutta, 1851.

[2] Colin, G., *Traité de physiologie comparée des animaux,* Paris, 1888, 3d ed., 2, p. 476.

[3] Evans, G. H., *Elephants and their diseases,* Rangoon, 1901 and 1910.

[4] Pütter, A., Arch. f. d. ges. Physiol., 1918, **172**, tables 2 and 3, p. 379.

[5] Mrs. Pütter has very kindly gone through many of Professor Pütter's manuscripts and found notes indicating that these observations were made directly by him, indeed, on several different animals of Hagenbeck's Circus. Unfortunately, the exact procedures of obtaining the heart rates were not noted in his protocols.

[6] Forbes, A., Cobb, S., and McK. Cattell, Amer. Journ. Physiol., 1921, **55**, p. 385.

Observations Made in 1935 on the Heart Rate of the Elephant

From this survey of the earlier reported heart rates of the elephant, it can be seen that Colin and Pütter are the only writers that indicate a heart rate in the vicinity of 30 beats per minute. All the others, Gilchrist, Evans, and Forbes, report heart rates of 40 beats or above. This discrepancy in the reported normal heart rates of an animal of as great physiological and zoological importance as the elephant necessitated a complete survey of the heart rate. Of prime importance is the method of obtaining the heart rate. Probably no single physiological measurement would be of any greater service to men responsible for the health and well-being of elephants than a simple method of obtaining the heart rate as an indication of febrile condition. Hence every effort was made to employ some simple technique for securing this observation. Attempts to carry out the recommended procedure of Gilchrist (subsequently stressed and repeated by Evans) to count the heart rate from the pulsation of the artery at the root or base of the ear resulted invariably in negative results. Repeated efforts were made to feel back of the ears of a number of the Ringling and the Barnes elephants, particularly the largest animals, and particularly when they were lying down and quiet. At no time could we assure ourselves of any reliable indication of a pulsation. Furthermore, the attempts at locating an artery near the base of the tail (a method of measurement that has been carried out with domestic animals such as the horse and the steer) proved unsuccessful. The general use of such a procedure, however, even if successful, would be debatable, for the artery at the base of the tail is without doubt located much deeper in the elephant and the skin surface over it is much harder, more leathery and less resilient and would not easily allow the impulse to come through. Furthermore, the elephant has tremendous power in the tail and could easily injure one's hand or fingers by drawing the tail closely to the body. Counting the heart rate by feeling of the pulsation of this artery might, therefore, be a fairly dangerous procedure, even with a well-trained animal. With large domestic animals we have been successful in counting the heart rate with the stethoscope. This, however, was unsuccessful when applied to the elephant, owing to its massiveness and its thick skin. The procedure recommended by Gilchrist of having a mahout trained to get the record was considered by Steel[1] especially difficult to carry out. Our own observations confirm Steel's impression.

Measurements of this type, however, are likely to cause considerable excitement in the animal. The high rates noted by Gilchrist, Evans, and Forbes, when compared with the long series of records (table 13, page 131) obtained by us by another method, indicate that the elephants were made somewhat apprehensive by the procedures employed, and that only when extreme care is exerted to avoid excitement on the part of the animal will the rate be normal. Because unable to obtain any satisfactory indication of the pulsation of an artery, we decided to follow the significant lead of Alexander Forbes and base our measurements upon the electrical current set up by the action of the heart itself. This electrical method, although technically complicated, is physiologically extremely simple and does not disturb the elephant in the slightest.

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[1] Steel, J. H., *A manual of the diseases of the elephant and of his management and uses,* Madras, 1885.

The Boas cardiotachometer[1] has been most successfully used in many researches at the Nutrition Laboratory and, with certain modifications, was found to be most satisfactory for the study of the heart rate of the elephant. Since we were interested only in the heart *rate,* we substituted for the recording device a highly sensitive Moll galvanometer with telescope, lamp, and scale, and to aid in dampening out extraneous currents several condensers (from 2 to 6 microfarads) were made available. The heart impulses could readily be counted from the galvanometer deflections. With this equipment and long electric leads preliminary tests were made at the Boston Zoological Park with, however, indifferent success, owing to the presence of a large number of stray electric currents in the building.

At Nashua, New Hampshire, our apparatus functioned perfectly, and our first accurate records of the heart rate of an elephant were noted on Benson's elephant, No. 4. The electrodes were extremely simple. They consisted of two sheets of zinc approximately 30 cm. square, attached to a plank about 1.5 meters long, with a space about 10 or 12 cm. between the plates. This plank was laid on the floor, with one plate connected to each lead of the apparatus, and the elephant was required to place her feet on this plank to give good conductivity. The electric conductivity could be, and was at times, bettered by putting a small portion of salt solution on the electrodes.

The apparatus was next transported to Franklin Park in Boston where, with the cooperation of Director Harkins and keepers Clark and Veasey, measurements were made on one of their elephants (No. 3). Here again there were so many stray electric currents in the elephant house that only when the apparatus was moved out to the asphalt-paved yard and changes were made in the electrodes could accurate measurements be obtained. A sufficient number of measurements to insure the true heart count of No. 3 were, however, ultimately secured. The other elephant, No. 2, was not deemed sufficiently tractable by the keepers to be placed in position with electrodes under her feet.

In the preparations to make an extensive survey of the Ringling herd in Florida, two more flexible and pliable electrodes were finally used at Franklin Park in place of the cumbersome plank. These were constructed of pieces of rubber matting approximately 18 inches (45 cm.) square, on one side of which was attached by leather thongs, in the form of a thread, a 14-inch (35 cm.) square of galvanized iron quarter-inch wire mesh. Between this mesh and the rubber padding were placed several layers of squares of cheesecloth, which could be moistened with salt solution. To make them less conspicuous to the elephant, who might be suspicious of their presence, these white pieces of cloth were darkened with ink. These flexible pads were found invaluable, for they could be shifted easily. This equipment was transported by automobile to Campgaw, New Jersey, where measurements were made on November 12, 1935, on the elephant Jap, who at that time had returned from her summer engagement. Unfortunately the day was damp, although Jap was under cover, and the stray currents from the innumerable electric light wires rather loosely strung around the grounds again caused a great deal of trouble; however, after numerous observations, sufficient records were obtained to secure accurate knowledge of the heart rate of this elephant. The whole equipment was then shipped to Sarasota, Florida, where it was placed near the quarters of the men, in the elephant enclosure. With leads 150 feet (45 meters) long, each elephant could be readily reached while it was in its quarters, chained to its own stake. By this means the heart rate of each of the thirty-four elephants when standing quietly was obtained.

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[1] Boas, E. P., Arch. Intern. Med., 1928, **41**, p. 403; Boas, E. P., and E. F. Goldschmidt, *The heart rate,* Baltimore, 1932.

At night a number of the elephants were measured after they had lain down, by having small brass gauze electrodes (15 cm. x 15 cm.) containing pads of cheesecloth moistened in salt solution held against the soles of the two front feet. A sufficient number that were not too disturbed by this process to lie quietly were measured to give a clear picture of the heart rate when the elephant is lying. In probably no instance were the animals in what might be called "profound slumber." They were not disquieted, but usually an eye would open and occasionally there would be a movement of the trunk or the foot, a movement instantly controlled by the voice of the attendant. Under these circumstances, therefore, the heart rates of eighteen of the Ringling elephants, while lying, were secured. Thus the total number of elephants whose heart rates were recorded, either standing or lying, was thirty-seven.

HEART RATE OF ELEPHANT NO. 4 AT NASHUA, NEW HAMPSHIRE

Heart rate in the standing position—On October 7, 1935, the unusually tractable and docile elephant (No. 4) at the Benson Animal Park in Nashua, New Hampshire, stood on the galvanized iron plates attached to the plank for various lengths of time and permitted a number of measurements. Since this was our first accurate study, unusual precautions were taken to secure a large number of counts on this animal. The elephant is naturally restless and does not stand in any one position for any length of time. This elephant was placed on the electrodes, counts began at the earliest possible moment, and were continued until the contact was broken. Obviously the longer the count, the more accurate is the calculated rate per minute. The time was usually recorded on a stopwatch to hundredths of a minute. The first series of counts gave the following results (time for each count not indicated):

Time	Beats counted	Rate per minute
11.00 a.m.	6	27
Shortly after this	20	27
A few minutes later	20	28

The contact was disturbed after the third count, but the observations were begun again at 11.10 a.m. In a number of instances thereafter a certain number of beats were counted, the time was noted at the end of a given count, and the count was then continued for a longer time. The calculation of the rate per minute in these instances, therefore, could be based not only upon the time for 15 beats, for example, but upon the time for 42 beats or even more. The continuous observations are indicated in the following data:

Time	Beats counted	Rate per minute
11.10 a.m.	9	28
Continued count	22	28
Shortly after this	16	27
Continued count	42	27

The barn temperature at this time was 12.5° C.

At 12.24 p.m. small pieces of sugar were fed to the elephant in an attempt to keep her on the electrodes as long as possible, and a continuous record was obtained as follows:

Time	Beats counted	Rate per minute
12.24 p.m.	7	28
Continued count	18	28
Continued count	26	29

Then the contact was broken. Three other sets of observations shortly thereafter showed:

Time	Beats counted	Rate per minute
	8	30
Continued count	18	29
	16	26
Continued count	28	26
Independent count	28	28

At 12.40 p.m. sixty-one consecutive counts indicated a rate of 28 beats per minute. It thus seems clear that elephant No. 4, under normal conditions (as regards feeding and well-being) and while standing, had a heart rate of not far from 27 to 28 beats per minute.

Heart rate in the lying position—At 1.08 p.m. elephant No. 4 was made to lie down by the keeper, but the floor of the barn, being of concrete and bare, was cold and the animal could not be made to remain lying for very long. She took a great deal of time to settle down into the lying position, and made a considerable effort in changing her body position. The wire gauze electrodes with cheesecloth inside of them (these moistened with salt solution) were held against the soles of the front feet by the trainer, Neuffer, who was wearing rubber gloves. The contact was satisfactory, and only one observation was made, which resulted in a count of 29 beats, showing a heart rate of 36 beats per minute. This indicated that the heart rate was higher when the elephant was lying than when she was standing. At the time this observation was made, it was believed that this difference was due to the considerable effort made by the elephant in lying down and the fact that the concrete floor was cold and she was uncomfortable. Subsequent observations on the Ringling herd in Sarasota, Florida (see page 133), confirm this remarkable difference between the heart rates in the lying and the standing positions.

Effect of exercise—Elephant No. 4 was next taken outdoors to the exercise ring and exercised vigorously for about six minutes. She was then brought into the barn and adjusted on the electrodes, which required about two minutes. The results of counts successively made were as follows:

Time	Beats counted	Rate per minute
1.20 p.m. Continuous series	22	37
	53	35
	70	35
	88	35
	100	34
New count at 1.28 p.m.	31	34
New count at 2.16 p.m.	59	30
Shortly thereafter	27	28
New continuous series	29	28
	39	28
	57	29
	71	28
	85	28

The last series of counts indicates that the elephant's heart rate had reached its normal level following the exercise. As a result of considerable exercise, therefore, from which the keeper was nearly "out of breath," the heart rate of this animal increased from a resting, standing level of 28 beats per minute to only 37 beats per minute. It should be borne in mind, however, that for the first two minutes following work the heart rate was not obtained. At the end of an hour after the work the heart rate was down to her normal rate of 28 beats per minute.

HEART RATE OF ELEPHANT NO. 3 AT FRANKLIN PARK, BOSTON

Precisely the same equipment used at Nashua, New Hampshire, was carried to Franklin Park, Boston, on November 6, 1935, and observations were there made on elephant No. 3. During the early experimentation in the forenoon, when the elephant was without doubt somewhat excited by the unusual procedure, a number of counts were obtained with the elephant standing, the maximum number being 21 and the minimum 7, with heart rates per minute ranging from as high as 33 beats to as low as 26 beats. This minimum rate is based on a count of only 7 beats, which took place in 0.27 minute. The stray electric currents in the building interfered so much that the equipment was moved out into the asphalt-paved yard, and the wire-gauze electrodes attached to the rubber mats were used.

In the early afternoon a large number of satisfactory measurements were made, showing rates in the standing position ranging from 22 to 28 beats. The details are as follows:

Time, p.m.	Beats counted	Rate per minute
1.21	20	22
1.23	24	24
1.25	27	26
1.27	12	26
1.28	19	28
1.29	26	26
1.30	17	26
1.32	18	26
1.34	28	26
1.38	16	28
1.42	15	28
1.44	10	26
1.45	14	26

The extremely low rate of 22 beats is based upon twenty continuous counts lasting 0.90 minute and hence in all probability is correct. One other record shows an unquestionably low rate of 24 beats per minute. On the average, the heart rate was 26 beats per minute or slightly lower than that of elephant No. 4. This latter elephant, however, was 11 years old or 29 years younger than elephant No. 3. The observations on these two elephants (having a considerable difference in their ages and with heart rates definitely below 30 beats per minute) indicate that the high values of 40 beats and over reported by at least three writers must have been obtained under conditions of excitement or agitation and are not true normal heart rates. Full confirmation of this conclusion could be had, however, only by studies with other elephants, preferably with a large herd.

HEART RATE OF THE ELEPHANT JAP AT CAMPGAW, NEW JERSEY

Since so many other physiological measurements had been made on the elephant Jap, it seemed desirable to study her heart rate also to complete, in so far as possible, the physiological picture of this animal. The conditions for the study (which was made on November 12, 1935) were by no means ideal, owing to the large number of stray currents and the damp ground. However, as a result of nine series of measurements between 11.32 a.m. and 1.50 p.m. a variability in the heart rates was noted of from 29 to 37 beats per minute. This irregularity was not observed with the other elephants. Jap was, for the most part, tractable and docile but required at times a certain amount of urging to place her feet on the electrodes and hold them there. The rates noted were as follows:

Time	Rate per minute
11.32 a.m.	35
11.33 "	32
11.33½ "	31
11.34 "	29
12.02 p.m.	31
12.30 " *	37 *
1.03 "	36
1.23 "	32
1.50 "	36

* Shortly after moved into position.

Jap, although apparently non-temperamental, nevertheless did show some variability in her heart rate. This irregularity may be in part ascribed to the fact that Jap was one of the first elephants whose heart rate was measured, and considerable experimenting was necessary in locating the electrodes and particularly in securing periods when the stray currents did not disturb. This same variability was strikingly shown subsequently by some of the elephants in the Ringling herd, indicating that the nervous excitement might be equally as important in increasing the heart rate as actual muscular movements, a phenomenon not infrequently noted with humans. Since five of the records on Jap show rates of 32 beats or below, it is reasonable to consider that her heart rate, when standing quietly and under normal conditions of feeding, was not far from 31 beats per minute.

HEART RATES OF THE THIRTY-FOUR ELEPHANTS OF THE RINGLING HERD IN FLORIDA

The reasonable uniformity in the heart rates found with elephants Nos. 1, 3, and 4 under conditions of quiet standing suggests that the high rates formerly recorded are without doubt abnormal. But because of the wide discrepancy existing between the previously published rates and our own records, the normality of the elephant's heart rate could not be considered to be established until a greater number of elephants were studied. The entire equipment was, therefore, transported to Sarasota, Florida, early in November 1935, and again with the intensive and ever helpful cooperation of Edward Doherty, the head elephant man, the heart rate (standing) of every one of the thirty-four elephants in the Ringling herd was obtained. The first series of measurements was made when the elephants were brought into the exercise court near where the apparatus was installed, led up to the electrodes, and made to stand upon them. The general impression was that the elephants were slightly excited by this procedure. Shortly after that the electrodes and leads were transported to a place near the usual standing positions of the elephants, near their own stakes in the barn. Installation of the apparatus here resulted in much less agitation, save in one or two instances when the elephants had been punished a short time previously for bad behavior by being "hooked" about the ankle. In these instances the command to place the feet upon a special electrode was apparently associated with the prior punishment. On the whole, however, the elephants were undisturbed by this procedure. The series of observations began on November 16 and continued through the night of November 20, 1935. The results obtained with the elephants in the standing position are recorded in table 13 and those with the elephants in the lying position in table 14. Each one of the values for the rate per minute is based upon at least eight or ten consecutive counts and frequently many more.

In general the elephants were most satisfactory and showed the effects of good training, in that they were controlled by the trainers and not, as is occasionally the case in zoological parks, the keepers controlled by the animals. Nevertheless, with a herd of thirty-four elephants, each with its own individuality most strongly shown, one can expect differences in reaction to the experimental technique. Some of the elephants were slightly agitated or uncertain, but this usually wore off quickly and is reflected in the tendency for the heart rates to decrease as the observations went on. Usually the entire session lasted only about fifteen to twenty minutes, frequently shorter than that. On the other hand, it is not always true that the lowest heart rates were the last figures recorded. Slight rhythms in attention or interest and the approach of a stranger would be reflected in the heart rate almost instantly, in spite of the fact that the elephant is a very large animal with a slow heart rate and accustomed to the continual presence of innumerable visitors while on the road.

Heart Rate in the Standing Position

In tables 13 and 14 it was deemed undesirable to include the innumerable minor notes made by the observers as these measurements continued.

Practically all of the seeming variability is explained by anxiety on the part of the elephant as to precisely what the procedure meant. Occasionally sudden rises in the heart rate are explained by the fact that the keeper had to bring the elephant back into place with a threatened hook movement, or by the fact that at times the elephant would trumpet and show definite excitability. Although these supplementary notes explain practically all the cases of variability shown in the tables, on the other hand at times there are very low counts that can not adequately be explained. Thus, the first heart rate of No. 21 on November 17, of 27 beats per minute (see table 13) was never again reached by this animal, and there is no explanation for this. Similarly there is no explanation for the low value for No. 15 on November 17, of 24 beats. This was based on a single count at 10.52 a.m. and was preceded by a rate of 29 beats at 10.51 a.m. and followed by a rate of 29 beats at 10.54 a.m. The two low values of 26 beats, which represent the first measurements on No. 35 on November 18, were not subsequently verified, and yet the times for these two counts (0.50 minute for 13 counts and 0.92 minute for 24 counts) confirm the accuracy of these observations. With No. 43 the second value, on November 18, of 24 beats was based upon six counts in a quarter of a minute. This low value may possibly be due to the very short counting.

These occasional very low rates without adequate explanation are of real significance when one attempts to draw off a statement as to the average minimum heart rates of these elephants, to be used ultimately in assessing a value for the *average* heart rate of the elephant, standing and on feed. It will be seen from the last column in table 13 that frequently the minimum observed heart rate may not be the same as that assumed as the average minimum heart rate. However, it is believed that, on the whole, the averages selected would be those that would have been obtained had a duplicate series of measurements been made.

Examination of the data in table 13 shows that the average minimum heart rates of a large majority of the elephants were 30 beats per minute or below, fully in conformity with that noted with No. 4 at Nashua. A slight correlation between the age of the animal and the heart rate is shown when these average minimum heart rates are plotted in relation to the estimated ages, as shown in figure 7. In this chart the numbers 2 and 4 against some of the plotted points indicate that at those particular ages two or four of the records showed heart rates at the same level. The elephants at the age of 20 years had, in general, a higher heart rate than those at 35 years and over. If a line were drawn through the plotted points on this chart to indicate the general trend of the data, there would be a slight tendency for the line to slope downward with the increasing ages. This comparison, however, disregards the temperament of the elephant (which, as has already been seen, plays an important rôle) and disregards the body weight. But the chart shows that the average minimum heart rate of the elephant, standing, might be accepted as being not far from 28 beats per minute.

The high value of 39 beats noted with No. 23 must be accepted with some reserve. This elephant was distinctly nervous when the test was made and

TABLE 13—*Heart rates of elephants (standing) at Sarasota*

Elephant No.	Date	Time	Rate per minute	Average minimum rate
	1935			
14	Nov. 17	4.48 p.m.	29	30
	Nov. 18	1.58 p.m.	32, 31, 31, 30, 30	
15	Nov. 17	10.45 a.m.	27, 30, 29, 24, 29, 30, 30, 30, 29	29
16	Nov. 18	1.03 p.m.	31, 31, 31, 31	31
17	Nov. 18	1.18 p.m.	31, 29, 33, 34, 34, 33	31
18	Nov. 18	11.15 a.m.	34, 32, 31, 31, 30, 30, 31, 28, 28, 36, 36, 33, 30, 28, 28, 29, 30, 31, 31, 31, 31, 31	28
19	Nov. 18	12.33 p.m.	27, 27, 26, 28, 28	27
20	Nov. 18	1.28 p.m.	29, 29, 26, 26, 26, 26, 26, 26	26
21	Nov. 16	5.21 p.m.	36, 40	32
	Nov. 17	10.27 a.m.	27, 32, 33, 33, 32, 30, 33, 32, 33, 33	
22	Nov. 18	1.07 p.m.	30, 29, 28, 27, 28, 29, 24, 24, 24	24
23	Nov. 18	1.38 p.m.	47, 46, 40, 46, 44, 43, 42, 38, 38	39
24	Nov. 17	3.13 p.m.	36, 33, 34, 34, 27, 35, 34, 32, 32, 32, 33, 35	30
	Nov. 18	2.22 p.m.	30, 30, 29	
25	Nov. 17	3.44 p.m.	36, 35, 34, 33, 35, 35, 35, 33, 33, 33, 33, 34, 33, 36	31
	Nov. 18	2.12 p.m.	38, 31, 32, 30, 31, 32, 32	
26	Nov. 17	11.44 a.m.	29, 29, 29, 31, 29, 29, 30, 30, 30, 28	29
27	Nov. 17	2.52 p.m.	37, 32, 31, 27, 31, 32	29
	Nov. 18	11.01 a.m.	36, 35, 34, 34, 33, 34, 32, 29, 29, 29, 29, 30, 29	
28	Nov. 17	11.58 a.m.	28, 28, 33, 34, 34, 33, 33, 33, 33	28
29	Nov. 17	2.04 p.m.	31, 31, 26, 26, 28, 27, 29, 29, 27	27
30	Nov. 17	4.01 p.m.	46, 43, 40, 31, 31, 39, 33, 33	30
	Nov. 18	2.02 p.m.	29, 30, 30	
31	Nov. 17	4.59 p.m.	31, 31, 29	28
	Nov. 18	1.45 p.m.	30, 28, 27, 28, 34, 33, 32, 32, 31	
32	Nov. 17	4.23 p.m.	29, 31, 31, 32, 34, 33, 33, 33	31
33	Nov. 17	1.20 p.m.	29, 23, 22, 23, 23, 23, 22, 23, 24, 24, 23	23
34	Nov. 18	11.33 a.m.	32, 31, 31, 32, 29, 31, 31, 31, 31, 33, 32, 32, 32	31
35	Nov. 18	12.00 noon	26, 26, 30, 29, 29, 30, 29, 29, 29	28
36	Nov. 18	12.39 p.m.	24, 22, 22, 22	22
37	Nov. 17	12.38 p.m.	27, 32, 27, 27, 27, 27, 28, 29, 28, 29, 29	27
38	Nov. 18	12.53 p.m.	36, 32, 32, 32, 32, 32, 31	32
39	Nov. 18	11.46 a.m.	32, 29	30
40	Nov. 17	3.28 p.m.	30, 29, 29, 38, 35, 33, 33, 33, 30, 30, 29, 30, 31, 31	30
41	Nov. 18	12.15 p.m.	30, 30, 29, 29, 28, 28, 27, 28	28
42	Nov. 17	10.14 a.m.	28, 26, 25, 27, 28	26
43	Nov. 18	12.28 p.m.	31, 24, 27, 28, 26, 26, 27, 26	26
44	Nov. 18	12.13 p.m.	26, 27, 27	27
45	Nov. 17	12.56 p.m.	41, 40, 34, 33, 33, 30, 32, 29, 30, 31, 30, 30, 29, 32, 31	30
46	Nov. 17	11.12 a.m.	29, 31, 29	25
	Nov. 18	12.45 p.m.	24, 25, 26, 26, 26, 25, 25	
47	Nov. 17	1.36 p.m.	36, 29, 28, 28, 28, 27, 27, 26, 26, 26, 27, 27, 26, 27	26

showed a disinclination to stay on the electrodes. She had to be forced into position, and it was noted that her right leg was quivering or shivering while the observations were being made. She was said to be a very nervous animal but, on the whole, with good intentions and ordinarily required little disciplinary action. Without doubt her nervousness at the time accounted for this particularly high value.

Even with the excitability connected with the novelty of these tests, values of 40 beats and above appear in the entire series of 338 records only in three counts with No. 30, in seven of the nine counts with No. 23 (whose generally nervous disposition has just been discussed), in one of the counts with No. 21, and in two of the counts with No. 45 (who had had to be chastised just prior to the observations). In no other case were rates as high as 40 beats noted. All these high values were the result of excitement incidental to necessary chastisement of the elephants. We are thus at a loss to understand how the rate of 49 beats per minute reported by Gilchrist (which he states is based upon "a very large number of measurements") and the rates of 46 to 50 beats reported by Evans can represent physiologically normal heart rates. Personal conversation with Dr. Forbes (who, as we understand it, was not in direct connection with the elephant but was in the room where the electrocardiogram was being taken) indicates that the high rate of 41 beats noted by him undoubtedly was ascribable to the fact that just previous to the heart-rate study the elephant had been actively exercising in the ring, in an exhibit performance in the yard of the Children's Hospital in Boston. Certainly the evidence as a whole shows that the heart rate of the elephant while standing is far nearer 28 beats than 46 or 50 beats.

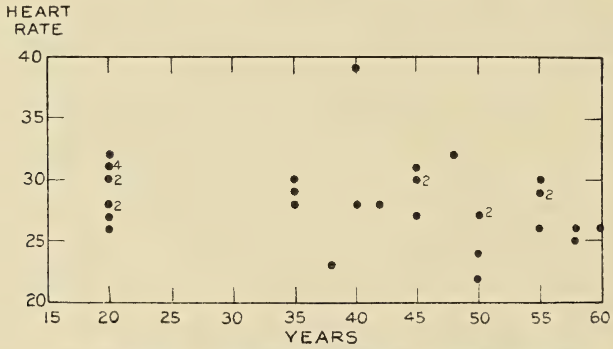

Fig. 7—Heart rates of elephants while standing, referred to age.

The numbers 2 and 4 against some of the plotted points indicate the number of identical heart rates noted at those particular ages.

Heart Rate in the Lying Position

The first observation on the elephant while lying was the single count on No. 4, which showed a higher rate in the lying than in the standing position. The general disposition of the elephant automatically to protect its trunk and feet when lying, particularly when asleep, made it questionable as to how electrodes could be applied. But the wire-gauze electrodes provided with pads of cheesecloth saturated with salt solution proved satisfactory. These were pressed against the soles of the front feet while the elephant was lying down and good conductivity was obtained, enabling a large number of readings. At times the electrodes were pressed against the elephant's feet by two observers, and hence no complicating, stray currents affected the results. When a single observer applied them, his hands had to be protected with rubber gloves. Many of the observations with the elephants in the lying position were made without undue excitement on the part of the animals, but in other instances the movements of the elephants were so unruly as to make records impracticable. None of the elephants would willingly injure the observer, and yet a sudden movement when one of them started out of a sound sleep could easily result in a serious injury. With eighteen of the elephants satisfactory records were obtained, and these are summarized in table 14. For purposes of comparison, the assumed average, minimum heart rates of these same elephants while standing are likewise given in the last column of the table. Usually these records were the results of numerous consecutive counts, never less than ten, and frequently twenty, thirty, or more. These counts were always taken after the elephants had been lying down for several minutes, to rule out the effect of the effort made by these huge animals in this major change in body position. The body position of the elephant is indicated by the letter R or L, to show whether the elephant was lying on the right or the left side when the counts were made.

TABLE 14—*Heart rates of elephants (lying) at Sarasota*

Elephant No.	Date	Time	Position	Rate per minute, lying	Average minimum rate, standing
	1935				
19	Nov. 18	10.22 p.m.	....	32, 32, 33	27
20	Nov. 20	4.00 a.m.	R	31, 35	26
21	Nov. 20	12.26 a.m.	R	34, 34, 34, 34	32
		4.10 a.m.	R	32, 34	
22	Nov. 20	1.32 a.m.	R	32, 31	24
27	Nov. 20	1.40 a.m.	R	36, 35	29
28	Nov. 20	1.00 a.m.	....	33, 33	28
32	Nov. 20	4.05 a.m.	L	32, 32	31
33	Nov. 20	1.10 a.m.	L	32	23
		3.04 a.m.	R	28, 28	
34	Nov. 20	1.47 a.m.	L	36, 39, (36)?	31
35	Nov. 18	10.28 p.m.	....	38, 36, 36, 36, 36	28
36	Nov. 20	3.53 a.m.	L	31, 31	22
38	Nov. 20	3.58 a.m.	....	34, 34	32
40	Nov. 20	1.56 a.m.	R	36, 39, 38	30
42	Nov. 18	10.36 p.m.	....	30, 30, 30	26
43	Nov. 20	1.27 a.m.	L	34, 32	26
44	Nov. 20	1.37 a.m.	R	40, 40, 38	27
45	Nov. 20	2.50 a.m.	R	42, 43, 44, 44	30
46	Nov. 20	1.30 a.m.	L	32, 32, 34, 33	25

It was not certain that the elephants were sound asleep when these observations were made. Indeed, the impression was that, for the most part, they were not in deep slumber. They were tranquil, however, and gave no indication of excitability or tendency to move. The striking feature of these observations is that *in all instances the heart rates of these elephants were more rapid when they were lying than when they were standing.* This finding is in full conformity with the single observation on elephant No. 4, but is strikingly at variance with what one would normally expect, since the heart rate is usually slower when a person or an animal is lying.

The unusual finding of a heart rate consistently higher when the elephant is lying than when it is standing is so at variance with our experience with all other animals that we find it difficult to explain. Even with large ruminants the heart rate is lower when lying than when standing. This is demonstrated by a series of observations on cows made recently by Professor E. G. Ritzman of the University of New Hampshire, in which care was taken to measure the animals not less than fifteen minutes after they had assumed either the standing or the lying position. The results are as follows:

Cow No.	Heart rate	
	Standing	Lying
1	60	52
2	58	51
3	56	48
4	62	52
5	62	48
6	56	48

Time did not permit a study of the heart rates of these elephants while they were lying first on the right side and then on the left side. The data in table 14 are too few to permit drawing any conclusion as to whether the particular side that the elephant is lying upon has any effect upon the heart rate. It is not inconceivable that when lying on the left side the elephant might have a more hampered heart movement than when lying on the right side. However, there are no satisfactory data to contribute information as to this point. Elephant No. 33 (normally having a low heart rate when standing of about 23 beats per minute) showed at 1.10 a.m. one count of 32 beats per minute, while lying on the left side and slightly restless. At 3.04 a.m., while she was lying on the right side, two counts gave heart rates of 28 beats per minute. This suggests that the heart rate is lower when the elephant lies on the right side. In both of these instances with No. 33, however, the rates were notably higher than the normal rates when the elephant was standing.

Need of a Simple Method for Recording the Elephant's Heart Rate

It is a matter of extreme regret that we are unable to suggest to the practical elephant man a simple method of obtaining the heart rate of the elephant, comparable to our suggested method of determining the body temperature. Every effort was made to find some artery that could be palpated to secure an index of the heart rate. In the case of the Ringling elephants the intelligent night watchman, James Ellis, convinced us that with one or two elephants, when lying down, he could note a sufficient pulsation in the upper chest to call off the pulsation at a tempo precisely in accord with that noted from our readings on the galvanometer. This procedure could not be duplicated with any of the other elephants while they were lying and with none when standing. Hence this apparently simple and practical method of counting the heart rate fails to be of real value.

Obviously an electrocardiograph technique or a technique comparable to our equipment is out of the question in elephant quarters. Time prevented attempting other techniques, such as the introduction of an inflated rubber ball into the large, capacious rectum and the suitable transmission of the pulsations to a tambour. Such observations are, however, very much to be desired, for it would be of invaluable aid to the elephant man and to the veterinarian to have not only a simple method of measuring the body temperature (which is now furnished, we believe, by the procedure outlined on page 149 for determining the temperature of the feces) but likewise a simple method of recording the heart rate. These two observations play a great rôle in the diagnosis and treatment of diseases of humans. Since a good elephant man has complete control over his animals, if some simple method of securing the heart rates of these animals could be secured, each elephant could readily be trained for such a procedure during health, to establish its normal heart rate. Later no difficulty would be experienced in making such observations during a suspected disturbance of well-being.

Weight of Heart in Relation to Total Body Weight

In Buchanan's interesting study on the pulse rate in vertebrate animals, emphasis has been laid upon the relationship between the weight of the animal and the heart weight.[1] Thus, from her own observations and from a survey of the literature she shows that in general "the more active animals have relatively the largest hearts and correspondingly the slowest pulses." She points out that the hen, weighing five times as much as the pigeon, has a heart weight amounting to 0.42 per cent of the body weight as compared with 1.5 per cent in the case of the pigeon, and that the frequency of the heart beat of the hen at rest is 330 per minute whereas that of the pigeon is 185 per minute. Among mammals the deer and the race horse have, relative to their size, especially large hearts, 1.15 and 1.12 per cent of their body weights, respectively, and Buchanan calculates that the heart rate of the deer in comparison with that of man would be about 45 beats per minute. With man she records the heart weight as representing 0.59 per cent of the body weight and the heart rate as being 70 beats per minute. With the hare having a heart weighing 0.75 per cent of its total body weight, the heart rate has been found to be 64 beats per minute, whereas with the rabbit, having a heart representing 0.27 per cent of its weight, the heart rate has been observed to be 205 beats per minute. Buchanan points out that the sparse data already available indicate the interest that would attach to the collection of a large number of facts with regard to this relationship, not only in different species but in different individuals of the same species.

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[1] Buchanan, F., Trans. Oxford Univ. Junior Scientific Club, 1909, n.s., No. 34, p. 351; Science Progress, 1910, No. 17, p. 60; Smithsonian Report, 1910, p. 487.

Pütter,[1] in discussing the relationships between the weights of the heart, the minute volume of the heart, the metabolic rate, and other factors, states that the observed heart weight in the case of the elephant is 0.44 per cent of the body weight and the observed heart weight of the whale is 0.508 per cent.

In our survey of the literature on the elephant and especially in our search for information regarding autopsies on this animal, data have been found regarding the relationship between the heart weight and the weight of the entire body. Vulpian and Philipeaux [2] examined the heart and lungs of a 33-year old female elephant and stated that the heart ("séparé des poumons, non préparé et non vidé") weighed 36 kg., but unfortunately they do not record the total body weight. Gilchrist [3] records a heart weight of 19.1 kg. with an elephant weighing 1975 kg., that is, about 1 per cent of the total weight. One wonders whether in the case of Gilchrist's animal the heart had been emptied of blood before being weighed.

In the case of Bolivar the heart weighed 19.1 kg. and the entire body 5440 kg. The heart was thus 0.35 per cent of the total weight. Kartoum, a somewhat smaller elephant, weighed 4710 kg., had a heart weighing 22.7 kg., or 0.48 per cent of the total weight. Mollie, a 40-year-old female elephant, whose heart was examined in 1921 by Dr. Paul D. White and Dr. C. S. Burwell (see page 113), weighed 3710 kg. and had a heart weighing 19.3 kg. The heart was thus 0.52 per cent of the total weight. On the average, if the exceptional case of Gilchrist's animal is not taken into consideration, the percentage relationship is 0.45. This is lower than the percentages recorded by Buchanan for any of the *large* animals listed in her table save the ox, which is credited with a heart weight percentage of 0.39.

Since Buchanan's articles were published, Laurie [4] has reported measurements made by Captain Sørlle at Stromness, South Georgia, in 1926 on a female blue whale. This whale weighed 122,004 kg. and the heart weighed 631 kg., or 0.51 per cent of the total weight.[5]

BODY TEMPERATURE

Rectal Temperature

Of the large number of animals whose metabolism has been studied, relatively few are devoid of protective covering; birds are provided with feathers and most other animals with fur or hair. Those without protective covering whose metabolism has been measured are the hairless mouse,[1] the pig, and man. Although humans are protected by clothing, metabolism measurements have been made upon them without it. Any of the large animals that have been studied thus far have had a reasonable protection of fur. The elephant, because of its almost complete absence of hair, is defectively insulated against cold and hence presents a problem from the standpoint of heat loss, particularly the paths for the loss of heat. Consequently its temperature regulation is a matter of special interest and any factors that might contribute information on this subject should be studied. Although the body temperature may be looked upon as merely the resultant of thermogenesis and thermolysis, it is not uniform in any animal but varies at different parts of the body. Nevertheless for comparative purposes body temperatures, particularly those taken deep in the body cavity, are of fundamental significance. Ordinary thermometry will hardly suffice for the study of the body temperature of the elephant. Evans has emphasized the importance of taking the body temperature of this animal and notes that as a general rule the temperature is slightly lower in the morning than in the evening. According to him the temperature of the normal elephant ranges from 97.4° to 98.8° F. or 36.6 C. Any temperature above this he considers indicative of fever, and a temperature of 100° F. indicates considerable fever. Evans relied upon readings of a thermometer held in the hand of an attendant, who inserted his arm, well lubricated, deep into the rectum and held it there for at least a minute. In such cases it was generally necessary to remove some dung from the rectum beforehand. A number of years ago Dr. W. Reid Blair of the New York Zoological Park informed us that with the Indian elephant he had found rectal temperatures of 97.4°, 97.2°, and 98° F. (36.2° to 36.7° C.).[2] Our own observations on the rectal temperature of the male African elephant, Kartoum, at this same park gave values of 35.90° and 35.85° C.[2]

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[1] Pütter, A., Arch. f. d. ges. Physiol., 1918, 172, p. 396.

[2] Vulpian, A., and J. M. Philipeaux, Ann. d. Sci. Nat., 4th ser., Zool., 1856, 5, p. 183.

[3] Gilchrist, W., *loc. cit.*

[4] Laurie, A. H., *Some aspects of respiration in blue and fin whales, Discovery* Reports, Cambridge, 1933, 7, p. 363.

[5] The heart of a young sperm whale 12 feet long has been reported to weigh 22 kg. The total body weight was not recorded. (See White, P. D., and W. J. Kerr, Heart, 1915-1917, 6, p. 207.)

The temperature of the elephant is rarely taken by practical elephant men. Hence special emphasis was laid in our study upon an attempt to make practical this physiologically important and pathologically highly important measurement. Various indices of febrile condition are used by practical elephant men in handling their animals. Thus Doherty tells us that he commonly examines the two small openings in the roof of the mouth just above the end of the lower lip, to see if they are free and clear. Dr. T. Wingate Todd tells us that these are the openings of Jacobson's canals. It is possible these may be important, not only as indications of temperature disturbances but as a landmark in measuring "length of trunk." If the elephant is in a normal condition, these openings are moist and wide open. If febrile, they are dry and closed. In this 1935 study no attempts were made by us to measure the body temperature in the rectum, but several series of observations were made on the temperature of the feces and the temperature of the urine, in the belief that the internal temperature of these large animals can be reasonably estimated from such measurements. In these series, several problems were carefully studied. Is the temperature of the urine the same as that of the feces and, if not, is there any consistent difference between them? Is there any difference in the temperature of the several boluses of feces in the order of their being voided, on the basis that the last bolus would have been deeper in the body and hence might possibly have a higher temperature? With repeated measurements is there any indication of a diurnal variation in the body temperature of the animal, as shown either by the fecal or the urine temperature? Were the rather considerable differences in environmental temperature experienced by Jap at Campgaw reflected in her urine temperatures?

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[1] Benedict, F. G., and E. L. Fox, Arch. f. d. ges. Physiol., 1933, **231**, p. 455.

[2] Benedict, F. G., Fox., E. L., and M. L. Baker, Amer. Journ. Physiol., 1921, **56**, p. 469; *idem.*, Proc. Nat. Acad. Sci., 1921, **7**, p. 154.

Feces Temperature

A number of years ago, in studying the skin temperature of Kartoum at the New York Zoological Park, we obtained a reasonably close approximation of the rectal temperature of the animal by plunging a thermometer into the center of a bolus of freshly dropped feces.[1] The temperature of this fecal mass was 36.2° C. With a female elephant at the same park a similar measurement gave a temperature of 36.7° C. In the first series of observations on Jap at Campgaw a few measurements were made of the temperature of the feces. With one of the Ringling elephants, No. 43, one such measurement was obtained on July 1. With the two elephants Nos. 2 and 3 at Franklin Park, Boston, observations were made on July 23 and on September 25. Feces temperatures with eight of the elephants in the Barnes herd were similarly measured on August 1, and an extensive series of observations with a number of the elephants in the Ringling herd were made in November 1935, in Florida. It was soon found that there was no consistent difference between the temperature of the first bolus and the temperature of the fourth, fifth, or even the sixth bolus. Consequently it is safe to assume that the temperature of any ball of feces is representative of the entire amount passed at that moment. This was clearly noted with Jap, with the Franklin Park elephants, and the Barnes herd.

The second, more elaborate study carried out in Florida gave identically the same picture. This study dealt with the temperature gradient in a bolus of feces itself, two clinical thermometers (with 0° correction) being used. One was inserted in the bolus about 35 mm. deep; the second was pushed in about 2½ to 3 inches, or 75 mm., allowed to stay half a minute or more, and then pushed in about 10 to 15 mm. farther. This was on the assumption that the relatively cooler glass (although the mass of glass and mercury in these thermometers is very small), when inserted into the feces, would cool the local particles of feces, but after the glass was warmed to the temperature of the bolus, it was pushed farther in and then assumed the real temperature of the interior of the bolus. With this in view, observations were made on the shallow and deep temperatures in eighteen balls of feces from eight elephants. These showed consistently that the deeply inserted thermometer recorded the higher temperatures. The average of all the temperatures, when taken deep in the ball of feces, was 36.6° C., and the average of an equal number of shallow temperatures was 36.0° C. Hence in any observations on the temperature of elephant feces it is important to follow the routine outlined above, first to insert the thermometer, allow it to remain where inserted half a minute, and then push it 20 mm. deeper, to obtain the true temperature.

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[1] Benedict, F. G., Fox, E. L., and M. L. Baker, *loc. cit.*

The temperatures of the feces of the twenty-four elephants studied are recorded in table 15. In eight instances (No. 21 on November 21, Nos. 22, 26, 30, and 33, No. 34 on November 19 and 20, and Nos. 45 and 46) the values in the fourth and ninth columns represent averages based upon measurements of the temperatures of from two to three successive boluses passed in one defecation. In all the other instances the values represent the temperatures of individual boluses. The average feces temperature of the twenty-four elephants was 36.5° C. Of special interest was the fact that the four measurements on Jap showed an average of 36.3° C., proving the strict normality of her feces temperature. The maximum temperature of feces passed by any individual elephant was 37.8° C. (100.0° F.), noted with the first of two boluses passed by No. 34 at 10.05 p.m., November 18. The second bolus had a temperature of 37.6° C., confirming the maximum temperature. Consequently we were interested in the results of observations on feces passed by this same elephant in the afternoon of November 19 when two boluses were found to have temperatures of 36.7° and 37.2° C. (average 37.0° C.). These two temperatures were quite within the range noted with the other elephants. On November 20 at 2.37 a.m. three separate boluses from this same elephant had temperatures of 36.7°, 36.3°, and 36.3° C. Apparently some transitory condition produced the relatively high temperatures on November 18 at 10.05 p.m.

Too few temperatures were determined during the night, but the data, so far as they lend themselves for a study of the influence of the time of day, suggest that there is no relationship between the variations in the feces temperatures and the time of day.

The average feces temperature of 36.5° C. for all the elephants is proof that the elephant's body (feces) temperature is essentially the same or slightly lower than that of humans, which is commonly stated to be 37° C.

It is the common custom of many hunters of wild game to note from feeling with the hand the temperature of a mass of feces, as a hint as to how long beforehand the game has passed. Dr. W. M. Mann of the National Zoological Park, at Washington, D. C., states that this is of special significance with elephants. Frequently the exterior of the bolus of feces of the elephant may have cooled off considerably; nevertheless, since the bolus is large, the heat in the center will be retained for a fairly long time, as can be ascertained by putting the hand in the center of the bolus. This retention of heat is undoubtedly due in large part not only to the initial heat of the mass but to prolonged fermentative action.

Urine Temperature

The urine of the elephant represents a large volume of fluid stored in a reservoir deep in the body cavity and hence presumably at the body temperature. The old idea of Stephen Hales[1] that the body temperature of

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[1] Cited by Pembrey, M. S., Schäfer's Text-Book of Physiology, London, 1898, I, p. 786, footnote 2.

TABLE 15—*Temperature of feces*

Elephant No.	Date	Time	Feces temperature	Average feces temperature
	1935		°*C.*	°*C.*
Jap	Mar. 16	9.37 a.m.	36.6	36.3
	" "	10.32 a.m.	36.4	
	Mar. 17	2.36 p.m.	36.1	
	Mar. 18	11.40 a.m.	36.2	
2	July 23	10.09 a.m.	36.6	36.7
	" "	11.50 a.m.	36.7	
	Sept. 25	9.55 a.m.	36.7	
3	July 23	11.03 a.m.	36.6	36.7
	" "	1.38 p.m.	36.8	
	Sept. 25	9.42 a.m.	36.6	
21	Nov. 15	5.43 p.m.	36.4	36.7
	Nov. 21	....	36.9	
22	Nov. 21	11.15 a.m.	36.2	36.2
24	Nov. 15	5.40 p.m.	36.7	36.7
	Nov. 21	10.50 a.m.	36.7	
25	Nov. 15	5.03 p.m.	36.6	36.4
	Nov. 18	9.38 p.m.	36.2	
26	Nov. 20	5.30 p.m.	37.2	37.2
27	Nov. 18	9.55 p.m.	36.2	36.5
	Nov. 19	2.00 p.m.	36.7	
30	Nov. 21	10.50 a.m.	36.6	36.6
	1935		°*C.*	°*C.*
33	Nov. 21	11.40 a.m.	36.3	36.3
34	Nov. 18	10.05 p.m.	[1]37.8	37.1
	Nov. 19	2.10 p.m.	37.0	
	Nov. 20	2.37 a.m.	36.4	
40	Nov. 18	9.40 p.m.	36.5	36.5
43	July 1	5.36 p.m.	35.9	35.9
45	Nov. 21	....	36.4	36.4
46	Nov. 21	12.15 p.m.	36.5	36.5
48	Aug. 1	12.44 p.m.	36.8	36.8
51	Aug. 1	1.55 p.m.	36.4	36.4
52	Aug. 1	3.25 p.m.	36.5	36.5
53	Aug. 1	5.07 p.m.	36.3	36.3
55	Aug. 1	5.58 p.m.	36.6	36.6
58	Aug. 1	5.15 p.m.	36.7	36.7
61	Aug. 1	6.08 p.m.	36.6	36.6
62	Aug. 1	4.55 p.m.	36.4	36.4
Average for 24 elephants				36.5

[1] A second ball of feces, measured a minute later, had a temperature of 37.6° C.

humans may well be taken by determining the temperature of the stream of urine as voided suggested that if the temperature of the elephant's stream of urine could be obtained, this should serve as a close measure of its true internal body temperature. With several elephants, therefore, the urine was collected in a wide-mouthed thermos jar and its temperature measured not with a thermal junction with instantaneous reading, which would have been preferable, but with an ordinary mercurial or quick-reading clinical thermometer. In making these measurements it was realized that several factors tend to lower the temperature of the urine as it is voided, and in so far as possible precautions were taken to guard against these. It is the custom of the female elephant, when urinating, to lower the external genitalia several centimeters, thus exposing them to the temperature of the surrounding air and contributing toward cooling of the urine, as passed. This is an unavoidable factor. There is likewise the possible cooling effect of the thermos jar in which the urine is collected. As the specific heat of the thermos jar is low, its hydrothermal equivalent in relation to the volume of urine collected is extremely small, and precautions were taken prior to collection of urine to fill the jar with water of approximately body temperature, it is inconceivable that there could be any significant loss of heat of the urine from its contact with the thermos jar. Invariably there is also in this method of collecting the urine a few moments of loss of heat from the urine, due to vaporization and radiation at the surface of the jar, but the temperature record can be made in such short time that it is hardly probable this vaporization and radiation can have any appreciable effect upon the temperature. Another possibility is that when the thermometer is introduced into the urine, the glass of the thermometer may of itself lower the urine temperature slightly. For this reason, in the measurements of the temperature of Jap's urine the thermometer was previously warmed by being kept in a thermos bottle of water at not far from 36° C. In the measurements on the Ringling, Downie, and Barnes herds and on the two animals at Franklin Park in Boston, however, rapidly registering clinical thermometers of small mass were employed, and these were not previously warmed. It was important not to have the temperature of the thermometer above that of the elephant's urine and as it was difficult to work in the field with precise water temperatures, it seemed better to disregard any possible cooling effect of the few grams of glass at never below 20° C. on the 400 cc. of urine at about 36° C.

Our final procedure in studying the urine temperature was to collect the urine in a wide-mouthed thermos jar (500 cc. capacity) that had been previously filled with water at about 36° or 37° C. At the instant when urination began, the water was thrown out and the jar was held under the stream of urine. When a large volume of urine was voided (but only under such conditions), the first jarful was frequently rejected and the jar filled again. As soon as the jar was filled, the thermometer (previously warmed or not, as explained above) was thrust into the urine and, after constancy was reached, the reading was made.

Owing to Jap's refractory disposition in reacting to the attempts to collect her urine (this was about the only instance where any irritability was shown by Jap), no total 24-hour collections could be made and but few continuous collections over fairly long periods. However, a number of urine temperatures were measured with the precautions outlined above. Six observations made in March were as follows:

	°C.
Mar. 15— 9.37 a.m.	36.3
Mar. 17— 2.28 p.m.	35.9
Mar. 17— 5.30 p.m.	36.3
Mar. 18—10.25 a.m.	35.6
Mar. 18— 2.20 p.m.	35.5
Mar. 18— 4.30 p.m.	35.3

In table 16 are given the time of day, the weight of urine, and the temperature of urine as recorded in the April or second series of observations on Jap. The weight of urine does not necessarily always represent the complete amount voided, for occasionally from 200 to 1000 grams (4000 gm. in one case) were lost. (See table 30, page 206.) In practically all cases, however, a sufficient amount was collected to measure the temperature in the thermos jar. The data regarding the weights of urine are of chief significance in their connection with the urine analyses (see page 204) but also have a bearing in the study of urine temperatures, for one is interested to know whether variations in these temperatures may be dependent either upon the barn temperature or the amounts of urine voided. Other things being equal, the larger the volume of urine, the more nearly one would expect its temperature to reflect the internal temperature, for if there is any cooling effect caused by the lowering of the external genitalia, this might be offset by the long-continued voiding indicated by the large weight of urine. Careful inspection of the simultaneously recorded barn temperatures does not show any influence of environmental temperature in the direction of a lower urine temperature with a lower barn temperature. If the environmental temperature affects the temperature of the stream of urine, either by cooling it directly or by cooling the external genitalia, a temperature depression in this direction would be expected. Comparison of the volume of urine with its temperature does not show consistently high temperatures with large volumes or consistently low temperatures with low volumes. It is highly probable, therefore, that these urine temperatures were correctly measured and not influenced significantly by barn temperatures or variations in the volume of urine voided.

The maximum and the minimum urine temperatures on each day in the April series of measurements on Jap are recorded in table 17, together with the difference between the minimum and the maximum and the average temperature on each day. In this 10-day study the lowest minimum urine temperature was 34.4° and the highest maximum temperature was 36.5° C., a complete range of 2.1° C. On any one day, however, the smallest difference was 0.6° and the largest 1.2° C. The conclusion is justifiable that the temperature of the urine of the elephant is by no means constant. It may vary 2° C. in the same animal in ten days' time and not less than a degree and at times over one degree in the same twenty-four hours.

The average urine temperatures on the different days range from 34.9° to 35.9° C. and the grand average of all the measurements (not weighting

TABLE 16—*Weights and temperatures of the urine of the elephant Jap*

Date and time of day	Barn temp.	Weight of urine collected	Urine temperature	Date and time of day	Barn temp.	Weight of urine collected	Urine temperature
1935	°*C.*	*kg.*	°*C.*	1935	°*C.*	*kg.*	°*C.*
Apr. 2				Apr. 7			
5.40 p.m.	11	5.13	34.6	3.50 a.m.	11	5.94	35.9
7.41 p.m.	12	2.99	34.8	5.35 a.m.	8	3.32	....
8.49 p.m.	11	5.69	34.9	8.58 a.m.	6	7.03	35.7
9.05 p.m.	11	6.05	34.8	11.42 a.m.	10	5.43	35.2
11.15 p.m.	11	9.05	35.3	1.35 p.m.	13	7.35	35.8
Apr. 3				5.20 p.m.	13	8.80	35.6
2.55 a.m.	15	.57	....	9.03 p.m.	11	7.79	35.6
4.18 a.m.	17	1.89	....	10.46 p.m.	10	5.46	35.9
5.58 a.m.	16	3.44	....	Apr. 8			
8.11 a.m.	10	4.38	....	12.30 a.m.	12	5.28	35.0
10.25 a.m.	12	4.82	34.5	3.50 a.m.	12	7.68	35.3
12.40 p.m.	12	6.02	34.9	6.54 a.m.	11	5.62	35.2
2.10 p.m.	12	4.51	34.4	8.46 a.m.	11	3.56	....
4.15 p.m.	12	4.62	....	12.10 p.m.	13	7.25	36.0
6.05 p.m.	10	5.70	34.7	3.40 p.m.	13	7.67	35.8
7.38 p.m.	9	3.15	34.5	6.50 p.m.	14	3.37	35.6
9.54 p.m.	10	5.30	35.5	9.14 p.m.	14	4.85	35.9
11.06 p.m.	11	3.03	36.0	11.45 p.m.	11	3.72	35.0
Apr. 4				Apr. 9			
2.21 a.m.	9	9.59	35.0	1.33 a.m.	11	3.35	35.8
6.00 a.m.	8	10.48	34.8	2.50 a.m.	10	3.15	36.0
8.49 a.m.	10	9.20	35.7	6.27 a.m.	10	8.74	36.0
9.46 a.m.	12	3.01	35.7	9.26 a.m.	9	5.10	35.8
11.10 a.m.	13	4.20	35.5	11.36 a.m.	9	3.29	36.0
2.14 p.m.	13	8.67	35.5	4.55 p.m.	13	5.65	35.6
5.39 p.m.	10	7.64	....	6.32 p.m.	11	4.81	35.5
6.46 p.m.	7	5.82	35.9	8.54 p.m.	9	10.72	36.1
7.25 p.m.	6	3.54	....	11.02 p.m.	9	3.40	35.9
7.59 p.m.	5	8.58	35.3	Apr. 10			
10.50 p.m.	9	8.03	36.0	12.19 a.m.	9	3.39	35.8
Apr. 5				1.59 a.m.	9	3.60	36.2
12.17 a.m.	9	4.36	36.5	4.45 a.m.	8	5.48	....
2.26 a.m.	8	6.11	35.9	9.15 a.m.	6	6.73	35.5
6.05 a.m.	11	10.15	36.0	1.20 p.m.	13	6.05	36.0
8.53 a.m.	12	6.78	....	4.35 p.m.	11	6.63	35.8
11.30 a.m.	11	4.51	....	8.38 p.m.	10	5.53	35.8
1.18 p.m.	10	3.85	35.8	10.08 p.m.	9	6.60	36.0
3.41 p.m.	10	4.07	35.5	10.45 p.m.	10	5.81	....
6.40 p.m.	10	4.28	35.7	Apr. 11			
7.59 p.m.	11	3.47	35.6	2.25 a.m.	11	8.90	36.0
9.53 p.m.	11	3.68	36.0	6.10 a.m.	10	7.12	35.9
Apr. 6				7.44 a.m.	9	2.85	35.6
12.09 a.m.	11	5.30	36.2	1.00 p.m.	14	6.18	35.6
2.25 a.m.	8	5.34	35.9	5.00 p.m.	11	3.59	35.1
5.46 a.m.	8	6.82	35.8	10.02 p.m.	13	7.07	....
8.05 a.m.	7	5.24	35.8				
11.36 a.m.	12	4.68	35.8				
2.18 p.m.	12	6.19	35.8				
5.24 p.m.	9	4.41	....				
8.19 p.m.	11	5.38	36.2				
11.52 p.m.	10	5.76	35.1				

the daily average values, which are based on from five to nine temperature readings each) is 35.6° C. This average is not significantly different from the average of the six urine temperatures on Jap in March (35.8°C.).

As has been strikingly shown with man and with certain animals, a diurnal variation in body temperature is the general rule. It was hoped to contribute to this point with the series of measurements on Jap in April. All of the urine temperatures were plotted with relation to the time of day, and the wide scatter of plotted points as indicated by the minimum and the maximum temperatures was noted. No definite trend with relation to the time of day, however, could be observed. Jap's sleeping was for the most part confined to the last half of the night. It is conceivable that could the measurements have been made while she was lying down, asleep, at night, there might have been a tendency for a lower temperature, as has been found with man, but there is no evidence to suggest that there was any significant diurnal variation in the body temperature of Jap.[1] This lack of evidence is perhaps explained by the animal's daily habits, for she slept only a few hours, had no bodily rest by lying down other than during these few hours of sleep, and in those instances when urine was voided immediately following sleep she stood up to urinate and the change in body position called for a considerable amount of muscular effort, tending of itself to raise rather than lower the body temperature. Continuous records of the body temperature by a thermo-electric couple deep in the rectum might have thrown some light upon this problem as to whether there is a diurnal variation in the elephant's temperature, but such observations hardly seemed justifiable in the exigencies of this field study.

Table 17—*Minimum, maximum, and average temperatures of the urine of the elephant Jap*

Date	Minimum	Maximum	Difference	Average
1935	*°C.*	*°C.*	*°C.*	*°C.*
Apr. 2	34.6	35.3	0.7	34.9
Apr. 3	34.4	36.0	1.6	34.9
Apr. 4	34.8	36.0	1.2	35.5
Apr. 5	35.5	36.5	1.0	35.9
Apr. 6	35.1	36.2	1.1	35.8
Apr. 7	35.2	35.9	.7	35.7
Apr. 8	35.0	36.0	1.0	35.5
Apr. 9	35.5	36.1	.6	35.8
Apr. 10	35.5	36.2	.7	35.9
Apr. 11	35.1	36.0	.9	35.6
Average	....	....	....	35.6

As can be seen from table 17, the low urine temperatures were found on the first two days of the April study and the higher temperatures on the succeeding days. In the thought that perhaps the time relation between the temperature measurement and the previous ingestion of water might play a rôle, this factor was carefully studied. No correlation between the time of water intake and the time of recording the first urine temperature thereafter could be observed. It is true that the measurements shortly following the drinking of water were below the general 10-day average of 35.6° C., but a large number of measurements taken a long time after water was drunk were also below this level.

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[1] A similar inspection of the Florida results gives no hint of a diurnal variation.

On June 18 one specimen of urine collected from No. 3, the older of the two elephants at Franklin Park in Boston, had a temperature of 35.3° C. On June 25 a specimen of her urine was collected in two jars, the first part of the stream being caught in one jar and the last part in another. The temperature of the first portion was 35.7° and of the second 35.6° C. A specimen collected in the same way with No. 2 showed a temperature of 35.7° for both the first and the second portions. On July 23 No. 2 was found to have a urine temperature of 36.3° both at 10.00 a.m. and at 12.35 p.m. With No. 3 on this same date the urine temperature was 35.9° both at 10.09 a.m. and at 12.45 p.m., and on September 25 No. 3 showed a urine temperature of 35.8° C.

TABLE 18—*Urine temperatures of Ringling elephants*

Elephant No.	Urine temperature	Elephant No.	Urine temperature
	°C.		*°C.*
14	35.5	29	35.7
15	35.7	30	35.7
16	35.8	31	35.9
17	36.0	32	35.7
18	35.8	34	35.8
19	36.0	35	35.7
20	35.9	36	35.6
21	35.8	37	35.6
22	35.8	38	35.9
23	35.7	39	35.9
24	36.0	40	36.3
25	35.7	41	35.9
26	35.5	42	35.6
27	35.9	44	35.8
28	35.4	45	35.4
Average of 30 elephants, 35.8			

With the Ringling herd an excellent opportunity was had of studying the urine temperatures of different elephants in Bangor on July first between 10.50 a.m. and 6.30 p.m. This study was supplemented later by observations on three elephants in Florida. The disinclination even for well-trained elephants to have an unusual proceeding take place toward the rear of the animal made the collection of these specimens very time-consuming and difficult. With great patience, however, thirty of the thirty-four elephants were measured. The values are reported in table 18, in which it can be seen that the lowest urine temperature was 35.4° C. in the case of two elephants, Nos. 28 and 45, and the highest 36.3° with No. 40. The urine temperature of No. 34, the elephant that showed a high individual feces temperature (see table 15, page 140), was 35.8° C. The average for the thirty elephants is 35.8° C. (96.4° F.) or exactly the average of 35.8° noted in one of the two series of observations with Jap. During the study with the Ringling herd, in several instances urine temperatures were recorded for the same elephant twice a day, usually in the morning and the afternoon. The all too few data suggest that there is no diurnal variation in the elephant's urine temperature, at least during the daytime, thus confirming the finding with Jap.

With the Downie herd on July 16 the temperature of the urine was noted in the case of only one elephant (No. 8) at 11 a.m. It was 36.0° C.

Urine specimens collected from eleven elephants in the Barnes herd (see table 19), between 12.43 p.m. and 6.19 p.m. on August 1, showed a range in temperature of from 35.7° to 36.2° and an average temperature of 35.9° C., which again agrees well with the averages noted with Jap and the Ringling herd.

TABLE 19—*Urine temperatures of Barnes elephants (Aug. 1, 1935)*

Elephant No.	Urine temperature
	°C.
48	36.1
49	35.7
50	35.7
51	35.7
52	35.8
53	35.9
55	35.8
56	35.9
57	36.1
58	36.2
59	36.1
Average	35.9

COMPARISON OF FECES AND URINE TEMPERATURES

Since before excretion both feces and urine are stored for a considerable length of time deep in the body cavity, it is natural to suppose that the temperatures of these two secretions will either be identical or will bear a fairly close relationship to each other. Although there is little, if any, evidence to show that the body temperature of the elephant varies from hour to hour in the nature of a diurnal rhythm, it is nevertheless obvious that the comparison of the temperatures of urine and feces can be made only when the collections of the two excreta are simultaneous or nearly simultaneous. Such close observations were made with twelve elephants, and for comparative purposes these are summarized in table 20, from which it can be seen that the temperature of the feces was in these cases from 0.2° to 1.2° C. higher than that of the urine. The average difference between these two temperatures is 0.7° C., a value which has definite practical application, as will be shortly considered.

This finding of a differential between the temperature of the feces and the urine of the elephant warranted study with other animals. Thanks to the kind cooperation of Dean L. S. Corbett of the University of Maine, and particularly his assistant, Mr. L. C. Plaisted, opportunity was given us to study the temperature of cows' feces and urine nearly simultaneously discharged. A second series of observations made on the cows in the dairy herd at the University of New Hampshire, with the kind permission of Professor K. S. Morrow, confirmed completely the results obtained at the University of Maine, namely, that there is a differential between the temperature of the feces (higher) and urine of the cow, but that it is measurably smaller than that noted with the elephant. With cows it is perfectly feasible to determine the rectal temperature. Observations made almost simultaneously on the rectal and feces temperatures of these cows showed that they were identical. As it is so difficult to determine the rectal temperature of the elephant, it is recommended that the temperature of the feces be used as an index of the internal body temperature when knowledge regarding this is desired.

TABLE 20—*Comparison of feces and urine temperatures*

Elephant No.	Date	Time	Temperature of		Excess in feces temp. over urine temp.
			Urine	Feces	
	1935		°*C.*	°*C.*	°*C.*
Jap	Mar. 16	9.37 a.m.	36.3	36.6	0.3
	Mar. 17	2.28 p.m.– 2.36 p.m.	35.9	36.1	.2
	Mar. 18	10.25 a.m.–11.40 a.m.	35.6	36.2	.6
2	July 23	10.00 a.m.–10.09 a.m.	36.3	36.6	.3
	July 23	11.50 a.m.–12.35 p.m.	36.3	36.7	.4
3	July 23	10.09 a.m.–11.03 a.m.	35.9	36.6	.7
	July 23	12.45 p.m.– 1.38 p.m.	35.9	36.8	.9
	Sept. 25	9.40 a.m.– 9.42 a.m.	35.8	36.6	.8
21	Nov. 15	5.43 p.m.	35.6	36.4	.8
27	Nov. 19	2.00 p.m.	35.9	36.7	.8
34	Nov. 19	2.10 p.m.	35.8	37.0	1.2
48	Aug. 1	12.43 p.m.–12.44 p.m.	36.1	36.8	.7
51	Aug. 1	1.55 p.m.	35.7	36.4	.7
52	Aug. 1	2.32 p.m.– 3.25 p.m.	35.8	36.5	.7
53	Aug. 1	5.07 p.m.	35.9	36.3	.4
55	Aug. 1	3.30 p.m.– 5.58 p.m.	35.8	36.6	.8
58	Aug. 1	5.15 p.m.	36.2	36.7	.5
Average			35.9	36.6	.7

The factors tending to lower the temperature of the urine and of the feces in any measurements of these temperatures were fully recognized by us and precautions were taken to have the technique of these measurements as accurate as possible, as explained on pages 138 and 141. The cooling effect of the thermos jar and likewise of the external genitalia could be avoided by measuring the temperature of the urine only when the volume of urine is large, under which conditions the thermos bottle could be filled several times and the temperature of only the last collection measured. This procedure, which was followed by us whenever possible, should certainly do away with any criticism of the accuracy of the urine temperature. Even if it is granted that there was a cooling effect of the thermos bottle in these measurements, one would suppose that this cooling effect on the urine might be offset by the cooling effect of the air around the bolus of feces. Since both materials come from the body cavity, the fact that the feces have a slightly higher temperature than that of the urine can logically be ascribed to the long period of time that food residues remain in the intestinal tract, undergoing fermentation with its resulting heat.

At the moment when food enters the mouth of an animal, particularly of a herbivore, it can be considered to have the temperature of the air surrounding the animal. But as this food passes into the intestinal tract, it is warmed by the body fluids and undergoes fermentation in the intestines. Its temperature is, therefore, increased not only by the warmth of the body into which it has entered but also by the heat of fermentation. Hence it is possible that the feces that pass through the alimentary canal have a temperature much above the cell temperature of the body, due to this heat of fermentation. That the differential between the feces and the urine temperatures is not so great with the cow as with the elephant may be explained by the large alimentary tract of the cow and the difference in the composition of the cow's feces. The food does not pass so rapidly through the intestinal tract of the cow as it does in the case of the elephant, and the fermentation takes place farther up in the tract, *i.e.*, the rumen, so that the heat of fermentation is to a large extent dissipated in the body before the feces reach the point of discharge. Furthermore, the semi-fluid nature of the feces of the cow might be another factor contributing to a somewhat more rapid dissipation of heat from the feces, whereas the large, almost solid bolus of feces of the elephant would lose its heat less rapidly to the surrounding intestinal walls and to the air, after defecation. The rapidity of passage of food through the intestinal tract, the intensity of fermentation, and the solid or fluid nature of the feces, therefore, all affect the temperature of the feces. These factors will be considered in further detail later. (See pages 185, 189, and 253.)

Because of the tremendous volume of urine discharged by the elephant, and because the thermometer was inserted into the urine instantly after its collection, it hardly seems possible that the urine temperature could have been influenced by the environmental temperature. The period of time that the discharge of urine was exposed to the air was but a fraction of a second and only the external part of the stream was exposed. In view of all these considerations the conclusion is justified that the records of the urine and feces temperatures of the elephant were correctly made and that the elephant's urine consistently has a definitely lower temperature by

0.7° C. (1.3° F.) than that of the feces, in all probability accounted for chiefly by the heat of fermentation.

CONCLUSIONS REGARDING FECES AND URINE TEMPERATURES

The digest of this entire series of temperature measurements shows that the temperature of the freshly dropped feces of the elephant, although varying considerably in the course of twenty-four hours (as noted in the study with Jap), can be considered on the average to be 36.5° C. In general the temperature of the urine is 0.7° C. lower than that of the feces. There is no significant difference between the temperature of the first bolus in the passage of feces and the temperature of the third, fourth, or fifth.

When the rectal temperature of a human is taken, care must be observed that the bulb of the thermometer is not imbedded in a mass of feces, for it is believed that this would give an erroneous reading. The question arises as to whether this same objection holds true with animals. The veterinarian, in determining the body temperatures of horses and cows, presumably takes no cognizance of the possibility of the presence of a fecal mass in the rectum. Evans has described a complicated method of determining the elephant's body temperature, which necessitates having a man insert his arm, holding a thermometer, into the rectum, after having first removed any feces present. It is not surprising that elephant men do not wish to do this. Comparison of the temperatures of urine and feces and determination of the temperature of the rectum after feces have been passed should be simple to make. In view of the findings in our study of the urine and feces temperatures of the elephant, and comparison of these data with rectal, urine, and feces temperatures of cows, however, it is believed that the difficulties presenting themselves in connection with rectal temperature readings can be avoided by taking the body temperature in another manner.

A PRACTICAL MEASURE OF ELEPHANT BODY TEMPERATURE

To practical elephant men desirous of keeping in touch with the physiological condition of their animals and wishing to utilize what is considered by the clinician as a most important index of physiological condition, that is, the measurement of body temperature, a relatively simple procedure is recommended. This involves the use of a standard clinical or so-called "fever thermometer," made by a reputable firm and preferably without correction factor.[1] This thermometer should be plunged into a bolus of feces, preferably a large one, *immediately after it has been passed.* The mercury bulb of the thermometer should be inserted in the bolus about 2 inches. At the end of half a minute it should be carefully pushed in still farther, until it is practically in the center of the bolus. After a further one and a half minutes, the thermometer is withdrawn and read. Since the temperature of the feces is higher than that of the urine, because of fermentation, it follows that the temperature of the urine is more nearly representative of the true body temperature. The difference is 1.3° F. (0.7° C.) on the average. Deduction of 1.3° F. from the feces temperature measured as just described should give, therefore, the *true* body temperature. Since the elephant defecates sixteen or more times in 24 hours, feces temperatures can be taken as frequently as desired.

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[1] These thermometers are self-registering and must be shaken down, prior to each reading, to well below 95° F.

Elephant men should familiarize themselves with this simple method of measurement, and note the *normal temperatures* or, more preferably, the normal range of temperatures of their various animals. In a vast number of cases the temperatures will be not far from those noted on tables 15 and 20, that is, on the average 97.7° F. (36.5° C.). In those cases where a notably higher temperature is found, the equivalent, for example, of 98.6° F. or more, the results should be immediately confirmed by two methods, one, by taking temperatures of feces in precisely the same way, using feces passed several hours later. If the temperature still remains high, a further control may then be made on the urine. For this purpose a slightly more elaborate technique is required, in that the operator should have a *wide-mouthed* thermos jar holding about a pint. The narrow-mouthed jar will not do. This is preferably filled with water at about 98° F., and just as the elephant urinates the warm water should be thrown out and the bottle held under the stream. If there is a large quantity of urine, it is preferable to throw out the first jarful and refill the jar. The temperature is then immediately taken by plunging the thermometer into the urine. This, compared with the feces temperature, should give a true picture of the animal's body temperature and fully confirm any high temperatures noted on the feces. Urine temperatures, however, need be taken only when, as will be rarely found to be the case, a temperature over 98.6° F. is found with the feces, and even then a second measurement of the feces temperature will almost invariably show values around 98° F. It is hoped that this extremely simple and hitherto unused procedure will enable the elephant man, the veterinarian, and men in charge perhaps of other types of animals to obtain direct indications of the body temperatures of their animals.

TEMPERATURE OF EXPIRED AIR

A novel technique only recently introduced with humans,[1] and until the time of our study on the elephant not used with animals, is the measurement of the maximum temperature of the expired air. In the act of expiration, air that has been for a long or a short time in the lungs is brought from the body. Naturally the temperature of this air is much higher than that of the air entering the lungs. Mercurial thermometers are not sensitive enough to record this temperature, since the period of expiration is so short, usually only a second or two. Hence a thermo-electric method is imperative, employing a very fine wire, copper-constantan, thermo-junction with thermostat and galvanometer. The use of this technique with the elephant has been described on page 25. The trunk of the elephant Jap was placed through the aperture in the wall of the respiration chamber (see A, Plates 2B and 4), the keeper held the trunk, and the junction (without protecting wires of any kind) was placed directly in one of the openings in the trunk so that the expiratory blast would blow over it. Successive readings of the deflections of the galvanometer were recorded until it was certain that the maximum temperature had been obtained.

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[1] Benedict, F. G., and C. G. Benedict, Science, 1934, **80**, p. 546.

Three such series of measurements of three separate expiratory blasts were made with Jap at 1.15 p.m. on March 17, at which time the temperature of the barn was 19° C. The results are as follows:

First blast °C.	Second blast °C.	Third blast °C.
28.3	30.6	29.5
27.6	28.4	26.7
28.9	29.0	30.3
27.8		
30.4		
28.0		
31.3		

The maximum temperatures of the three blasts were 31.3°, 30.6°, and 30.3° C., respectively, averaging 30.7° C.

With elephant No. 4 at Nashua, New Hampshire, measurements were likewise made of the temperature of expired air in several exhalations. The measurements of individual blasts were as follows: 29.1°, 26.3°, 28.7°, 29.8°, 28.9°, 30.4°, and 30.3° C. Although the average of these values is 29.1° C., it is obvious that the highest temperature, 30.4° C., more nearly represents the temperature of the air exhaled from the lungs. This value is essentially that found with Jap, but the barn temperature at Nashua at this time was 12.5° C. as compared with 19° C. at Campgaw.

In Florida, on November 19, 1935, at about 1.00 p.m., measurements of the temperatures of a number of expiratory blasts were made with three of the Ringling elephants, with the following results:

No. 42—32.3°, 32.7°, 32.6°, 32.8°, 32.0°, and 32.3° C.
No. 32—32.3°, 31.5°, 31.2°, 31.4°, 31.5°, and 31.2° C.
No. 15—31.8°, and 31.5° C.

With No. 42 the highest temperature was 32.8°, with No. 32 it was 32.3°, and with No. 15, 31.8° C. The average maximum expired air temperature of the three elephants was 32.3° C., or only from 1.6° to 1.9° C. higher than those noted with Jap and elephant No. 4, although the barn temperature in Florida (25.3° C.) was notably higher than at Campgaw or at Nashua. Hence the higher temperature of the air entering the lungs of the Ringling elephants affected only moderately the temperature of the air leaving the lungs.

With three elephants the temperatures of the expired air were likewise noted shortly after they had drunk large amounts of water of a temperature of 23° C. In the case of No. 42 the expired air temperatures were 30.6°, 31.7°, 31.6°, and 31.2° C. The maximum value, 31.7°, was 1.1° below the highest temperature before the water was drunk. In the case of No. 15 values of 30.3°, 29.7°, and 30.2° C. were recorded. The highest was 30.3°, that is, 1.5° C. lower than the highest temperature noted before the water was drunk. With No. 20 temperatures of 30.5° and 31.0° C. were found after she had drunk water. In her case no measurements were made prior to the drinking of the water, but the maximum temperature afterwards, 31.0° C., is lower than any of the values found with the other elephants before water was taken. Thus the drinking of water has a noticeable effect upon the temperature of the expired air, as is to be expected from the fact that these large volumes of water are taken through the trunk.

As a matter of fact, the temperatures of expired air following water intake were not invariably measured immediately after the elephant finished drinking, but at times several minutes had elapsed.

With humans it has been established that the maximum temperature of expired air is higher with forced exhalation than it is with normal breathing and is almost one degree (Centigrade) below that of the simultaneously recorded rectal temperature. In the case of the elephant the difference between the maximum temperature of expired air and the probable rectal temperature is more nearly 6° C., and the maximum temperature of the expired air is very low when compared with that of humans. The anatomical structure of the elephant is such, however, that obviously the temperature of the air expired through its trunk would probably be much lower than the expired air temperature of any other animal. The elephant inhales air mostly through its proboscis, which is two meters or more long. The proboscis is a relatively small amount of the total body tissue, although it is highly vascular. As air enters the proboscis it is cold and relatively dry, takes up moisture from the mucous lining of the proboscis, and thereby cools it. When the warm, moist air from the lungs is exhaled, it must pass through this long, previously moderately cooled trunk before it finally issues at the end of the trunk. Thus it appears that the trunk itself plays a considerable rôle in the mechanics of heat loss of the elephant.

In a survey made of the temperature of the tip of the trunk of elephant No. 42 it was found that the temperatures at two different points on the outside of the trunk, about 5 cm. from the end, were 29.0° and 29.2° C. One measurement was made of the internal temperature, about 8 cm. from the tip, and showed a temperature of 30.1° C. In the case of elephant No. 42 the temperatures of the tip of the trunk, both inside and outside, were essentially the same as the skin temperatures at other exterior parts of the body (see page 157) but measurably lower than the temperature of the expired air. The trunk is, therefore, a considerable factor in heat loss.

The amount of heat expended by the elephant in warming the inspired air from a temperature corresponding to that of the environment to the temperature at which it is discharged from the trunk may be calculated approximately from the data that are available for Jap. Thus, the average ventilation of the lungs of this elephant was 310 liters per minute (at 0° C., dry, and 760 mm.). (See page 121.) In her particular case the temperature of the air in the barn was 19° C., and the maximum temperature of the expired air was 30.7° C. Thus it was necessary to warm the inspired air 12° C. Since a liter of air weighs 1.293 grams, 310 liters would weigh 400 grams. The specific heat of air is 0.237. Thus 400 grams of air are the equivalent of 95 grams of water. If 95 grams of water are warmed 12° C. per minute, this would correspond to 1.14 calories per minute or 1642 calories per 24 hours. Since the basal heat production of Jap (see page 281) was 49,000 calories per 24 hours, this means that 3.4 per cent of the heat produced was expended in warming the inspired air to the temperature at which it was discharged.

Similar calculations for humans have been made and show that under ordinary conditions 1.5 per cent of the heat given off by a man at rest is given off in the process of warming the expired air.[1] With most of the humans, however, the calculations have been based not upon direct measurement of expired air but on the assumption that expired air has a temperature of about 34° C. This value, we distinctly believe, based upon the experience at the Nutrition Laboratory with humans and with the expired-air-temperature measuring apparatus, is definitely about 4° C. too high.

Skin Temperature

The elephant, by reason of its lack of fur covering, presents a relatively simple surface for the study of skin temperature. In spite of the irregular and horny, hard nature of its skin, there are many points on its surface where sufficient contact with a thermo-junction can be obtained to register what is approximately the skin temperature. In any study of the factors governing the heat loss of various animals, the area and the nature of the integument should be taken into consideration. The elephant is of particular interest from this standpoint because it is the largest hairless land animal, and hence it is reasonable to compare measurements of its skin temperature directly with measurements on humans who are defectively covered with hair and artificially protected by clothing.

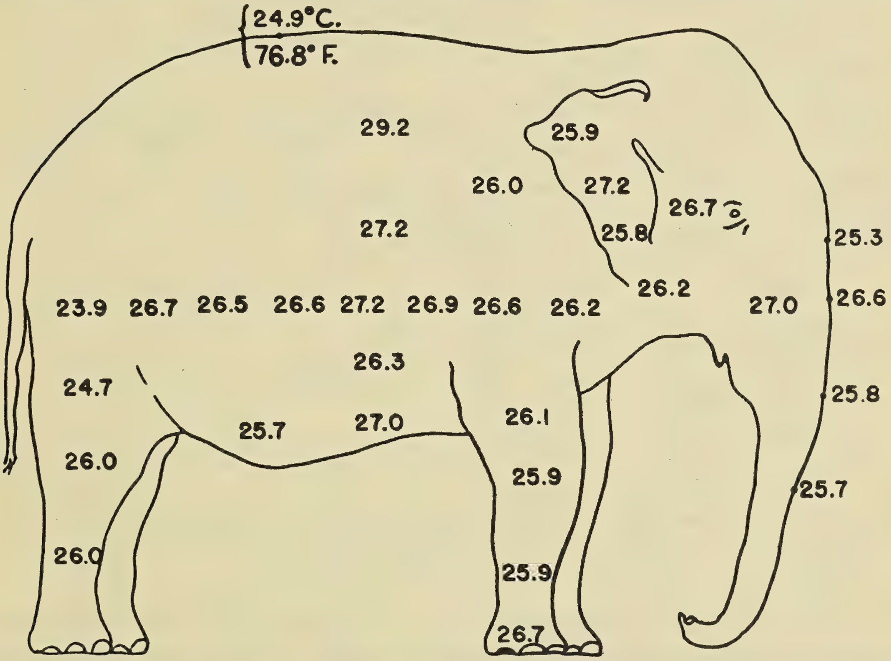

FIG. 8—SKIN TEMPERATURES (°C.) ON THE RIGHT SIDE OF THE FEMALE INDIAN ELEPHANT JAP. Temperature of environment, 16° C.

OBSERVATIONS ON THE ELEPHANT JAP

With Jap a few observations of the skin temperature were made on March 17 between 3.53 and 4.03 p.m. The thermo-electric method employed for this purpose (which has found extensive use with humans) has been described on page 25. For this study arbitrary marks were made on Jap's skin, and the temperatures were determined at these various points. The results are shown in figure 8. Since it was impossible for the trainer to make Jap lie down or get down on her belly, it was impossible to make an adequate study of the temperatures on the back. Jap did get down on her knees for a moment, but in a strained position, so we had to content ourselves with only one measurement on the back.

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[1] Rubner, M., Bethe's Handb. d. normal. u. pathol. Physiol., Berlin, 1928, 5, p. 155.

The barn temperature at the time these measurements were taken was 16° C. For twenty-four hours before it had ranged from 23° to 14° C., being on the average about 17° C. These were sensibly higher tempera-

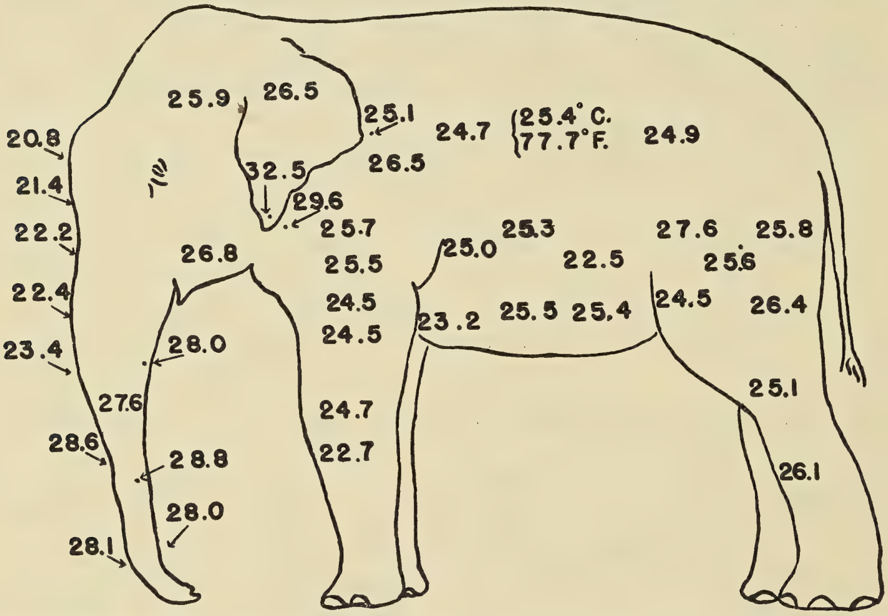

Fig. 9—Skin temperatures (°C.) on the left side of the female Indian elephant Alice at the New York Zoological Park.

Temperature of environment, 19.5° C.

tures than those that had prevailed during the preceding week. The wind, although not very cold, was blowing strongly, and in spite of the fact that an attempt was made to keep the doors of the barn closed, there was much more movement of wind in the elephant barn than there would be, for example, in an elephant house in a zoological park. To what extent this influenced the skin temperature of Jap is difficult to state, but this factor should be considered in any assessment of the values.

As can be seen from the measurements shown in figure 8, there was, on the whole, remarkable uniformity in the temperature of the skin on all parts of the body, the extremes being only from 23.9° on the rump to 29.2° C. on the upper part of the flank. Three skin temperatures not shown in figure 8 were as follows: 27.8° in the groin under the right leg; 29.6° behind the right ear, and 29.5° C. a little higher up behind this

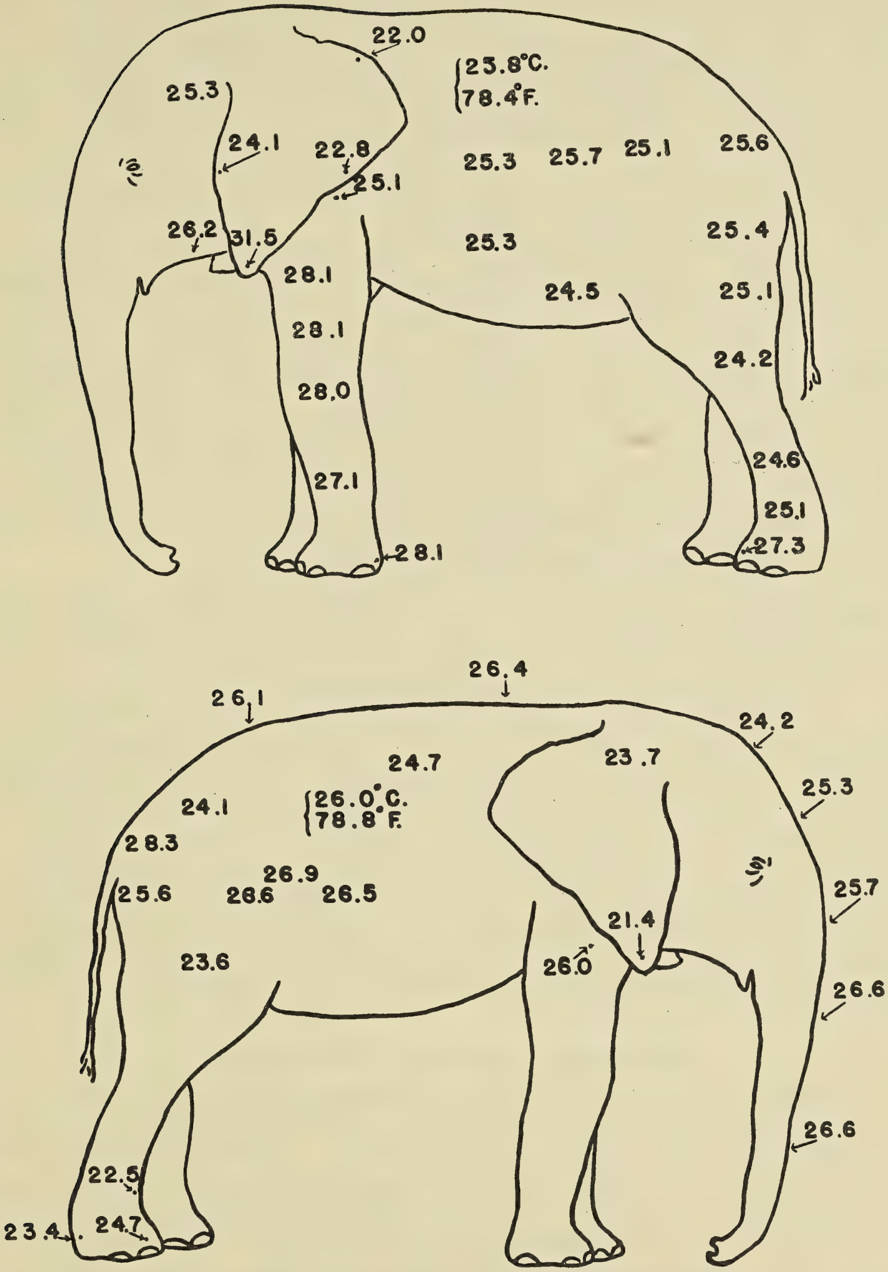

Fig. 10—Skin temperatures (°C.) on the left and right sides of the male African elephant Kartoum, at the New York Zoological Park.

Temperature of environment, 19.5° C.

same ear. The average of the entire series of temperatures is 26.5° C. Because of the uniformity in the surface temperature of Jap one can argue (assuming a direct radiation of heat to the environment) that the heat lost from this animal was singularly uniform per square meter of body surface, almost irrespective of which part of the body was exposed. On several occasions, however, when feeling with the hand in the right axilla and between the right axilla and the right breast, the impression was received that this part of the body was warmer than the rest, although by no means as warm as one might expect.

Study at the New York Zoological Park in January 1921—Previous to the observations on Jap the Nutrition Laboratory had already made some skin-temperature measurements on elephants at the New York Zoological Park.[1] In figure 9 are shown the temperature measurements on the female Indian elephant, Alice, at the New York Zoological Park, and in figure 10 those on the male African elephant, Kartoum. These animals had been living for several weeks, if not months, at a singularly constant environmental temperature close to 20° C. On the average their skin temperature was 25.5° C., or one degree lower than that noted with Jap. However, in some instances their skin temperatures (especially those on the ear) were notably higher than the temperatures found with Jap.

Although Jap's skin temperatures were studied at a time when the barn temperature was close to 16° C., it was shown by the recording, integrating thermometer that for at least a week before these measurements Jap had been subjected to a much colder environment (as low as 10°, 5°, and even 0° C.) during the nights. How quickly the naked animal will adjust its skin temperature to a higher environmental temperature one does not know (probably fairly quickly), but the change in the environmental temperature must be taken into consideration in the comparison of the average skin temperature of Jap with that of the two New York elephants. Since there was only one degree difference between the average skin temperatures of these animals, it can be concluded that Jap had apparently adjusted herself rapidly to the environmental temperature of 16° C. and that the observations on her confirm the earlier observations, namely, that the average skin temperature of elephants at environmental temperatures between 17° and 20° C. is about 25° or 26° C.

OBSERVATIONS ON FOUR RINGLING ELEPHANTS

The skin-temperature apparatus was transported to Sarasota, and measurements were made on four of the Ringling elephants on November 19, 1935. The barn temperature at the time was 25.3° C. The skin temperature was measured at fourteen arbitrarily chosen points on the body. The locations of these points are shown in figure 11, and the actual temperature values are recorded in table 21. The temperatures, for the most part, are close to 30° C., varying from this by only one or two degrees. The average for No. 21 is 29.1° C. No. 15, on the other hand, had a skin temperature higher than 30° C. at all points but one on the body, and her average was 31.5° C. With No. 20 the temperatures were about 31°, but with No. 42 they were

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[1] Benedict, F. G., Fox, E. L., and M. L. Baker, Amer. Journ. Physiol., 1921, **56**, p. 464; *idem,* Proc. Nat. Acad. Sci., 1921, **7**, p. 154.

TABLE 21—*Skin temperatures of Ringling elephants at Sarasota, Florida (Nov. 19, 1935)*

Location of measurement[1]	Elephant No.			
	15	20	21	42
	°C.	*°C.*	*°C.*	*°C.*
Trunk				
1	31.0	30.2	29.1	30.0
2	31.6	31.6	30.7	30.4
3	32.7	32.8	32.0	31.4
Ear				
4	30.9	30.1	27.8 & 26.1	29.1
5	33.0	32.3	29.1 & 31.1	31.5
Other parts of body				
6	31.9	30.1	29.0	29.6
7	32.6	30.5	28.9	29.8
8	30.8	27.9	27.9	30.0
9	31.2	30.2	28.3	29.6
10	31.4	31.5	28.1	29.8
11	30.6	30.8	28.9	29.9
12	29.7	30.0	28.3	29.7
13	32.5	30.9	28.9	29.1
14	31.4	30.5	29.9	29.9
Average	31.5	30.7	29.1	30.0

[1] See figure 11, page 157, for exact location of these measurements on body.

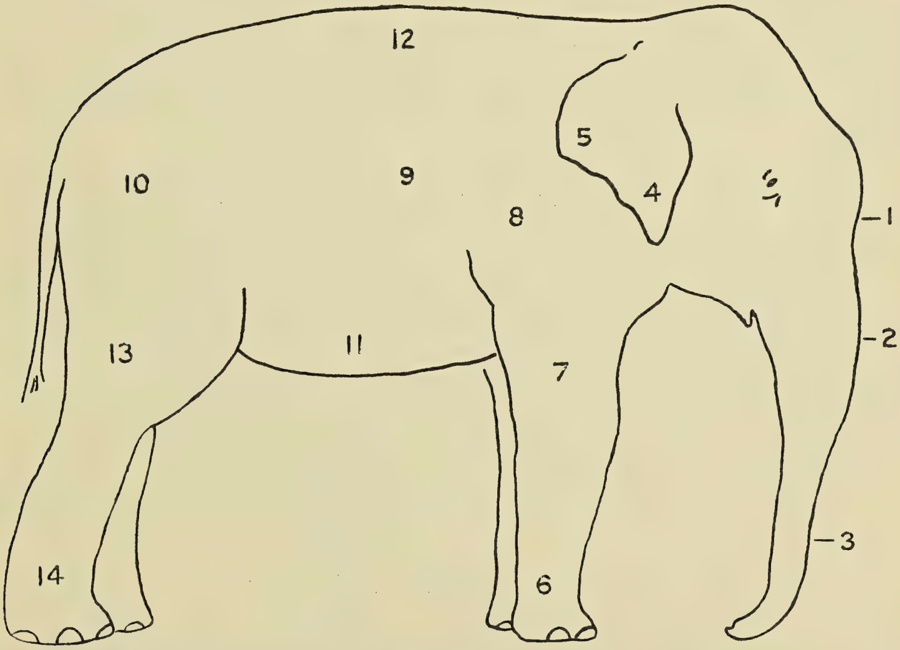

FIG. 11—OUTLINE OF ELEPHANT'S BODY, SHOWING LOCATION OF SKIN-TEMPERATURE MEASUREMENTS ON FOUR RINGLING ELEPHANTS.

Numbers were arbitrarily assigned to the different points of measurement on the body. The actual skin temperatures at these numbered points are reported in table 21.

a little lower, averaging 30° C. The general average for all four elephants is 30.3° C. (86.5° F.), a skin temperature measurably above that found with Jap and with the New York elephants. This difference is accounted for in large part, however, by the fact that the environmental temperature in the case of the Sarasota elephants was nearly six degrees above that of the New York Zoological Park elephants and nine degrees above the environmental temperature when Jap was measured. The general uniformity of the skin temperatures at all the points measured on the bodies of these four Ringling elephants again suggests that there is a reasonably uniform heat loss from this surface, which is unprotected by fur and hence open to direct radiation.[1]

EAR TEMPERATURES

With elephant No. 4, at the Benson Animal Farm, it was noted that directly following vigorous exercise in the ring there was an increase in the temperature of the ear. In the case of the Ringling herd, on the other hand, after the exercise incidental to their short ring performance no noticeable increase in ear temperature was observed with any of the animals. These observations were unsatisfactory, however, inasmuch as they were made only by the crude method of feeling of the ear with the hand. With the Barnes herd opportunity was had to study the elephants following *severe* muscular work. Feeling of the ears and then placing the hand on the shoulder or any other part of the body showed a much warmer temperature on the ear, although thermometric measurements could not be made. A striking fact brought out by this method of comparison was that when the entire row of eighteen elephants was observed in this manner, one animal was found to have normal skin temperatures on the ears. This seemed an extraordinary situation until it was explained that this particular animal had not done any work.

The rise in ear temperatures noted with the Barnes herd following muscular exercise thus fully confirms the earlier observations at Benson's park on No. 4. This apparently emphasizes again what has been pointed out by Hesse [2] and a number of other writers, namely, the seeming importance of the ears of the elephant as a heat-regulating mechanism. Certainly with severe muscular work the temperature of the ears increases perceptibly. On the other hand, higher temperatures on the sides of the ear than on other parts of the body were actually measured with the thermo-junction in the case of Alice and Kartoum of the New York Zoological Park, and yet these elephants were well housed and almost inactive. In the case of Alice, extreme nervousness approximating fright might have accounted for this phenomenon, but Kartoum was entirely indifferent to our presence and to the measurements. The rôle that the ear may play in heat regulation has already been considered to some extent in the discussion of the activity of the elephant, particularly as regards the motions of the ears, trunk, and tail. (See page 65.)

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[1] The elephant can absorb a considerable amount of heat from the sun. For example, one late afternoon, when the sun was low, its rays came under the edge of the canopy and struck on the foreheads of the elephants on one side of the barn. Even several minutes after the sun had gone down, as one went along the line one could feel that the foreheads of these elephants were still warm. This indicates that these animals must absorb a great deal of heat from the sun, when standing in direct sunlight. It also emphasizes the fact that elephants, in accordance with the best practises in India, are supposed not to be exposed to direct sunlight for any length of time and accounts for the fact that they generally inhabit the forests and seek the shade, when possible.

[2] Hesse, R., Zeitschr. f. wiss. Zool., 1928, 132, p. 314.

In addition to the fact that the ear temperature rises after muscular work, it has been observed by many that the ear movements are very rapid, that elephants flap their ears more than usual when they come from the ring, and these ear movements are referred to as fan-like effects to control the temperature. Przibram[1] claims that the tail is a great heat-regulating factor in the case of the rat, but one can not conceive of the tail of the elephant, in spite of its continuous activity, as being a factor in heat regulation. Our belief is that the elephants are psychologically excited after their ring performances and that the ear *movements* as well as the tail movements are in large part merely a nervous reflex and can not play any great rôle in heat regulation.

The relative thinness of the ears and the fact that they are readily frozen (Jap's ears were mutilated by frost) demonstrate that the ears are extremely sensitive and that when there is blood flow to the ear, relatively great heat losses may then take place. Our frequent observations on ear temperatures (to be sure felt only with the hand in the case of the Ringling herd) led to the conviction that the ears rapidly assumed a higher temperature when there was an element of nervousness, fright, or apprehension, even when the elephants were not doing any particular exercise or work and were not subjected to an especially warm environment. (See page 158.) In a number of instances immediately after the elephants had been chastised the ears were felt with the hand, and a definite increase in temperature was noted. Thus it would appear as if the ears were extremely sensitive and capable of rather rapid changes in blood flow. But these changes in blood flow are, in all probability, ascribable not to a true heat-regulating mechanism in the ears but rather to a nerve reflex, as exhibited by the elephants when rapidly flapping the ears during a period of excitement. That a large, hairless animal, unprotected by fur, needs any special temperature-regulating device in its ears is inconceivable. The ears of the rabbit have frequently been referred to as an example of the use of the ear as a thermo-regulator. But the rabbit is heavily furred, is often subject to danger and fright resulting in excessive muscular activity, and for these reasons such a thermo-regulating device would have its advantages. The elephant, on the other hand, is rarely subject to undue fright except when hunted by man, as he has no other enemies, and the absence of fur would make for the least insulation. Consequently we believe that the theory that the elephant's ears serve as an important heat-regulating mechanism is not tenable.

FOOD

Because of the size of elephants it is not surprising that they eat large amounts of food. But even allowing for their great size, any one noting their feeding habits, in India when they are grazing, in African wilds where they have passed through, or in zoological parks or circuses where they are in captivity, can not but be impressed by the literally enormous amounts of food necessary for these animals. In captivity, especially under conditions prevailing in the United States, elephants are fed on three different nutritive levels. In the zoological parks they are given the best of care, and undoubtedly the feeding there is most scientifically carried out. The standard feed, hay, is supplemented at regular intervals by grain, bread, green vegetables (chiefly carrots and mangels), bran, and salt. For the benefit of the elephants the directors of the various zoological parks make use of all the information available on the feeding of these animals, including the knowledge derived from modern research on the importance of vitamines. In the circuses, when on tour, the best herds are given excellent care and feed. On tour the animals are fed mainly hay, occasionally vegetables, and periodically bran. The Ringling and especially the severely worked Barnes herd are likewise given a liberal supply of bran and oats. Salt is given every second day. When in winter quarters elephants, especially those in the smaller groups, receive fairly scant rations. They are carried through the winter much as the thrifty farmer winters his stock, that is, on the lowest possible food level, for the economic phase plays an important rôle in the very heavy expense of feeding the elephant. Frequently elephants are given hay alone during the winter season, and it has been reported that in some cases they have been wintered on dried corn stover.

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[1] Przibram, H., *Temperatur und Temperatoren im Tierreiche,* Leipzig and Vienna, 1923, p. 63.

A study of the feeding of wild and tame elephants, with positive information only regarding feeding in captivity, has been made by Schrempp.[1] Of special interest is Schrempp's citation of the reports by Hagenbeck,[2] Krumbiegel,[3] Grabowsky,[4] and Priemel,[5] regarding the rations of elephants maintained in zoological parks. These reports show in all cases that there is a preponderance of hay in the diet and the frequent use of bread and beets. Schrempp himself studied the food intake of a 3000-kg. female Indian elephant, Matschi, for five weeks. During this time the animal received per day 2.2 kg. of bread, 3.55 kg. of oats, 3.23 kg. of bran, and 30.34 kg. of hay. These rations illustrate the effort made by zoological parks to give animals an adequate diet, not only from the standpoint of calories but from the standpoint of salts and vitamines.

Each of the two elephants at Franklin Park in Boston is fed daily about 100 pounds of hay, 1 to 1½ pecks of vegetables, ten loaves of bread and 4 quarts of bran.

So far as circus elephants are concerned and specifically in the case of the Ringling herd, approximately 3400 pounds of hay were fed to the thirty-four animals daily at the time of our observations, representing on the average 100 pounds per animal. This exact amount was not received by each animal, however, for obviously the larger ones needed more than the smaller. Whether the larger elephants ate faster and thus obtained a larger share is not known, but there apparently is no prearranged method for supplying more hay to the larger animals. On one occasion, after the show at night and after the audience had left the menagerie, a bale of hay was rolled up in front of the middle of a row of five elephants, side by side. Before the wires of the bale could be cut, all five were reaching out with their trunks, pulling off bits of hay. When the wires were cut, the hay was kicked about by the attendant, apparently without any definite planning, and pulled around by the elephants. There was no indication of unruliness among the elephants. Every other day the Ringling elephants receive bran and oats, not far from 10 to 15 pounds for each animal, or about 400 pounds for the entire herd. The concentrates, although having a definite food value, are given chiefly to keep the elephants free from constipation. Once a week carrots are fed. The quantity fed is not known, but at least they receive in this vegetable some vitamines. Salt is usually given along with the bran and oats.

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[1] Schrempp, W., *Betrachtungen über den wilden und den zahmen Elefanten unter besonderer Berücksichtigung der Fütterung und Haltung des letzteren,* Diss. Hannover, 1934, pp. 32-33.

[2] Hagenbeck, C., *Von Tieren und Menschen. Erlebnisse und Erfahrungen,* Berlin, 1908.

[3] Krumbiegel, J., *Wie füttere ich gefangene Tiere?* Akademische Verlagsgesellschaft, Leipzig, 1933, p. 17.

[4] Grabowsky, *Der Futtermittelverbrauch im Zoologischen Garten zu Breslau im Jahre 1904,* Zool. Garten (Breslau), 1905, Jhrg. 16, p. 1.

[5] Priemel, K., *"Ipani," die portugiesisch-ostafrikanische Elefantin des Frankfurter Zoo.,* Zool. Garten, 1930, 3, p. 241.

The Barnes herd of animals, which are characterized by doing a great deal of severe muscular work, had food before them most of the time and ate all they wished. Trainer McClain informs us that for the eighteen elephants each day two tons of good hay are fed. In addition, they have 500 pounds of grain mixed with 300 pounds of bran. This is mixed and moistened, and then salt is added. The salt is given at the rate of a little more than 10 pounds a week for the entire herd. Considerable stale bread is also given to them and occasionally cabbage, carrots, etc. The hay is fed five times a day, and the concentrates about twice a day. In winter quarters, except when the elephants are actually doing work, they are given bran but once a week.

The nine elephants in the Downie herd, animals measurably smaller on the whole than those in the other two herds, received about 700 pounds of hay daily, and twice a week a mixture of 3 bushels of bran and 5 bushels of oats. Twice a week, along with the bran and the oats, salt was fed, the total amount for the nine elephants and the four camels in the Downie menagerie being 10 pounds.

Circus elephants, when on tour, likewise receive considerable extra food from the spectators in the form of peanuts, popcorn, and the like. Indeed, peanuts are a distinct asset to the circus owner, entirely aside from the profit of the concessionaire, and this fact is taken into consideration in the feeding of circus elephants.[1] Park animals likewise are fed extensively on Sundays by the visitors, so much so that a curtailed ration is purposely given to them on Sundays. At the circus visitors usually pass before the animals for about one hour between 1 and 2 o'clock in the afternoon, again between 7 and 8 o'clock at night, and for a short time after each performance, perhaps from 5 to 5.30 p.m. and from 10.30 to 11 p.m. The constant supply of food given to the animals during these periods contributes to the incessant intake of some kind of food material throughout the twenty-four hours, and there is no rhythm in the feeding habits of these animals. The extra food thus obtained is not the same, however, for all elephants in a circus herd. Thus, in the general arrangement of the line of Ringling elephants, when the writer saw them, the largest animals were at the head. The spectators, as they came in, naturally stopped to feed these elephants first, and hence the peanut bags were fairly empty by the time the visitors reached the end of the line. The food received from visitors did not play such a rôle in the case of the Barnes herd, for they were tethered so that it was difficult for them to get their trunks far enough forward to reach the peanuts and popcorn.

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[1] This point is emphasized by Schrempp (*Betrachtungen über den wilden und den zahmen Elefanten unter besonderer Berücksichtigung der Fütterung und Haltung des letzteren,* Diss. Hannover, 1934, p. 34), whose data for a 5-week feeding period show that the Sunday rations were curtailed to allow for the food the visitors gave to the elephant.

The amount of food given to circus elephants on tour evidently is sufficient, for they all look in good condition. The Barnes herd particularly, although hard-working animals, all looked plump and well at the time of our observations, so apparently they must have been receiving all they wanted to eat.

The food habits of Jap, the animal upon whom our most extensive study was made, had apparently been extraordinarily irregular, depending in large part upon the financial success of the different enterprises with which she had been associated, as is the case with all animals in captivity. It was reported that in recent years there had been great changes in the nature of her food and that one owner had maintained her for much of one winter in the south on corn stalks alone, because he did not have money to buy other food. Our chief interest, however, was in her food for the few months preceding our study and during the time of our study. Apparently just prior to the observations at Campgaw she had been fed exclusively hay. When in a New York stable she received a very poor quality of baled hay, and no green vegetables were fed. The impression is that she ate one bale of hay per day here, that is, about 120 pounds, although the stories with regard to the amount of hay eaten vary greatly. When she was on tour in the summer and had considerable work to do, such as pushing mud-stuck vans out of circus lots and pulling tent stakes, she is said to have eaten three bales of hay daily, with occasionally some bran or oats.

When Jap was in winter quarters at Campgaw, at the time we studied her, she was fed almost exclusively hay and certainly not in liberal amounts. This was the situation throughout the entire time we were associated with her. Furthermore, the hay, when sampled and sent to Durham, was assessed by Professor Ritzman as being of inferior quality and cut very late. Occasionally Jap received small tidbits from the few visitors who appeared and on the days when she was inside the respiration chamber liberal amounts of bread to keep her quiet. This was day-old, sliced bread, of which she was very fond. In the first respiration experiments she had nearly a bushel daily. As the experimental season progressed, however, the keeper gave her less and less bread, because he knew it was desirable to study her inside the chamber as nearly as possible without food. The bread, therefore, was a distinct luxury and not a part of her regular fare. During the day when the trunk-breathing experiments were made (March 17) about 6 pounds of lump sugar were fed to Jap. Occasionally popcorn, an orange, or potato peelings were fed to her; otherwise no other supplementary food was given during our period of study. She received no vegetables, no grain, and no salt at any time throughout the winter. No green stuff was available in the barn or outdoors under the trees, to which she was occasionally chained.

The hay fed to Jap at Campgaw during the first series of observations on her was given loose, in unweighed amounts. The keeper simply went over to the hay barn, periodically, and came back with a good-sized forkful of hay. The statement was made at that time that she was fed an extra amount to keep her quiet and to prevent her from kicking the barn over. During our second series of observations, however, baled hay was used to some extent, and a complete record was secured of all the hay eaten during the 9-day period beginning at midnight on April 2 and ending at midnight on April 11. The keeper with a forkful of hay was weighed on a platform scale sensitive to within 10 grams, then after the hay was fed to Jap the man and the fork were weighed, and the weight of the hay was determined by difference. The time of each feeding, the individual amounts of hay given to Jap, the amounts of hay not eaten, and the few food accessories given during this 9-day period are recorded in table 22. The hay wasted was collected not at the time of each individual feeding but at intervals throughout the nine days. Thus, between 1.15 p. m. on April 4 and 4.55 p.m. on April 5 Jap wasted 9.39 kg. of hay and between 4.55 p.m. on April 5 and 11.07 a.m. on April 7, 5.15 kg. The total amount of hay given to Jap in the nine days amounted to 490.73 kg. Of this 41.65 kg. were wasted, leaving 449.08 kg. that were eaten. This represents a daily consumption of hay, on the average, amounting to 49.90 kg.

A sample of the hay was taken at each feeding and placed in a bag, so that at the end of the nine days a composite sample was available representing a sample of each feeding throughout the entire period. This bag unfortunately was not weighed at the time, as it should have been. It was subsequently weighed at the Nutrition Laboratory, and the changes in weight due to atmospheric conditions were carefully noted. Thus the weight of the bag plus the hay was 2.41 kg. after the hay had been in the Laboratory for several days. It was then taken outdoors into the garage, where it was damp, and there it gained 90 gm. or 3.7 per cent in one day. It was next taken back to the Laboratory under normal conditions of heating and ventilation, and there it remained until it had regained constancy in weight, at which time the weight was 2.40 kg. It was put out in the garage again and increased in weight, after three weeks, to 2.52 kg. The material as weighed after it had been in the garage three weeks was considered to be in the same state as it was when fed to Jap, for the conditions in the barn at Campgaw where the hay was stored were fairly comparable to those existing in the garage at the Nutrition Laboratory. On the basis of these observations, together with data on the changes in weight of the burlap bag in which the sample of hay was stored, it is possible to make a reasonable correction in the determination of the moisture in this hay to take care of the difference

TABLE 22—*Food eaten by the elephant Jap, April 3 to 11, 1935*

Date and time	Hay	
	Individual feedings	Not eaten
1935	*kg.*	*kg.*
Apr. 3		
8.45 a.m.	13.69	
11.35 a.m.	4.08	
6.35 p.m.	(1)	
6.42 p.m.	46.50	
Apr. 4		
2.30–3.30 a.m.	(2)	
11.05 a.m.	(3)	
1.15 p.m.		1.18
3.20 p.m.	.79	
4.22 p.m.	3.29	
4.34 p.m.	5.13	
7.40 p.m.	26.81	
Apr. 5		
2.25 a.m.	10.38	
11.46 a.m.	(1)	
4.55 p.m.		9.39
5.05 p.m.	4.75	
5.35 p.m.	9.78	
8.34 p.m.	22.80	
11.36 p.m.	5.43	
Apr. 6		
12.30 a.m.	2.85	
5.46 a.m.	1.40	
10.00 a.m.	12.28	
12.42 p.m.	6.83	
3.20 p.m.	4.55	
3.45 p.m.	(5)	
4.32 p.m.	2.02	
6.40 p.m.	16.33	
10.25 p.m.	8.20	
Apr. 7		
12.30 a.m.	6.83	
1.30 a.m.	3.33	
3.30 a.m.	3.92	
7.41 a.m.	2.09	
8.37 a.m.	2.17	
8.55 a.m.	1.85	
9.40 a.m.	3.22	
11.07 a.m.		5.15
11.08 a.m.	1.90	
1935	*kg.*	*kg.*
Apr. 7 (cont'd)		
11.25 a.m.	2.25	
12.15 p.m.	1.70	
1.18 p.m.	2.72	
1.48 p.m.	2.21	
2.20 p.m.	18.69	
6.42 p.m.	25.39	
Apr. 8		
3.46 a.m.	2.70	
7.23 a.m.	1.67	
7.55 a.m.		4.80
9.33 a.m.	5.41	
10.30 a.m.	(4)	
11.42 a.m.	6.25	
4.40 p.m.		9.02
5.20 p.m.	6.67	
10.00 p.m.	4.30	
10.20 p.m.	9.70	
Apr. 9		
12.20 a.m.	33.34	
7.00 a.m.		6.14
1.45 p.m.	20.71	
7.40 p.m.	29.55	
Apr. 10		
2.05 a.m.	3.92	
9.37 a.m.	9.62	
11.35 a.m.	11.04	
3.00 p.m.		4.42
6.00 p.m.	6.79	
6.55 p.m.		1.32
11.58 p.m.	8.83	
Apr. 11		
1.14 a.m.	7.61	
8.02 a.m.	3.90	
8.10 a.m.		.23
8.45 a.m.	(6)	
11.45 a.m.	2.52	
1.44 p.m.	6.12	
2.45 p.m.	(7)	
5.09 p.m.	9.79	
6.06 p.m.	5.20	
7.00 p.m.	8.93	

[1] Bread with 10 pieces of rubber.

[2] Ate hay used for pillow.

[3] Ate 1.81 kg. potato peelings.

[4] Bread with 5 pieces of rubber.

[5] Ate 0.88 kg. apples.

[6] Bread with 4 pieces of rubber.

[7] ¼ lb. (113 gm.) sugar.

in the moisture content of the hay as actually eaten by Jap and that of the sample of hay at the time it was subjected to chemical analysis.

This composite sample of hay (timothy) was, through the kindness of Professor E. G. Ritzman of the University of New Hampshire, analyzed to determine its chemical composition. From determination of the moisture content of the hay as received for analysis at Durham, with correction for the difference in the moisture content of the hay as fed to Jap in the barn at Campgaw, it is calculated that the water-free substance in the hay eaten amounted to 45.89 kg. per day, that is, that the hay as fed contained 8.0 per cent moisture. On the water-free basis the hay contained 4.23 per cent ash, 1.133 per cent nitrogen, 1.89 per cent crude fat, 36.38 per cent crude fiber, and 4.5 calories per gram. Analysis of a sample of this same hay for its sodium-chloride content, made at the Nutrition Laboratory, showed that it contained 3.92 mg. of sodium chloride per gram of water-free substance.

It is believed that during this 9-day period when the total hay intake was measured, Jap was on a ration probably not far from that on which she was accustomed to be wintered. The relatively low amount of food given in the 9-day period from April 2 to 11 suggested that at least during the winter season for a considerable period of time Jap does not receive a maintenance ration. Yet in spite of the unscientific, one-sided ration of relatively poor hay, with no concentrates and almost no food accessories, she certainly looked as if she had plenty of fat on her and presented an extraordinarily good physical appearance, equal to, if not better than that of any of the elephants seen by the writer in the zoological parks visited in Boston, New York, Philadelphia, or Washington.

It was reported that Jap had been given no vegetables, bran, or salt for many weeks. Evans points out that in India each elephant should have access to approximately two ounces of salt each day. At the New York Zoological Park salt is continually at hand, and the animals eat it as they wish. On the road the circus herds are regularly fed salt, but apparently it is common to neglect the feeding of salt and vitamines with animals not on tour. This seeming neglect of food accessory substances, coupled with the apparently poor digestibility of hay in the case of the elephant, at least as shown by the macroscopic examination of the feces (see page 177), indicates that the method of feeding elephants is wholly empirical. An intelligent study of this feeding problem would be of considerable value both in prolonging the life and sustaining the health of these animals and probably from the financial standpoint.

Use of bran by the elephant—The common custom of elephant men of feeding their animals bran or oats is found, on discussion with them, to be primarily not to furnish calories but to physic or "keep them loose." This custom of feeding roughage in the bland and finely prepared diet of man has been used extensively to prevent constipation. The introduction, however, of oats and bran into a diet made up of coarse roughage, such as hay, puts an entirely different aspect on the nature of bran as a laxative. When one considers the enormous mass of undigested or but slightly attacked hay that passes, in large pieces, through the intestinal tract and appears in the bolus of the feces of the elephant, it seems inconceivable that the undigested bran particles could have any effect whatsoever from the standpoint of mechanical irritation. Consequently we are forced to the conviction that there is some specific laxative factor in bran quite aside from any possible mechanical effect on the intestinal tract. In studies with domestic animals it has been shown that the laxative properties of bran are not ascribable probably in even a small part to the roughage therein. It is all the more striking, therefore, to find that bran is given to the elephant whose mastication is so defective that the hay in the feces represents probably coarser material than passes through any other known animal's intestinal tract. This emphasizes, we believe, the non-importance of roughage *per se* in the matter of constipation. The regular use of bran by elephant feeders, except in the case of Jap, proves that the laxative properties of bran are superimposed upon the large masses of very coarse, fibrous material which otherwise passes through the intestinal tract.

In the light of our digestion study with Jap and our macroscopic examination of the elephant feces (see pages 177 and 192) it is believed that the feeding of elephants is capable of considerable revision and should be a matter for serious contemplation. This species of animal is normally accustomed to feeding in the wild on succulent material. The elephant is an animal of the forests rather than the plains. In the wild it leads for the most part a nocturnal life. In Africa, especially, its food is in large part leaves and young shoots (bamboo shoots and green grass in India) and practically no dried grasses make up its diet. In captivity, especially in America, the food is in large part, if not wholly, dried grass or hay. The digestive tract of the captive elephant must accommodate itself to this wide difference between the native or normal diet and the diet in captivity. It is perhaps surprising that this adjustment has been as perfect as it is. That man's selection of food for the elephant is the wisest from the physiological or even the economical standpoint is open to debate. It is hoped that in the following chapters of this book the findings reported may be of some service in solving this problem.

Although hay is a staple food for the elephant in captivity in America, there are various kinds of hay, and even with the same kind of hay there are great differences in quality and digestibility. The digestibility of various grades of timothy hay, for example, has been found to differ according to the period of cutting the hay and, indeed, with different normal animals.[1] Fortunately much information is available regarding the digestibility of these so-called "roughages," obtained in careful experiments on sheep, horses, and particularly cows and steers. These variations in digestibility are so apparent that it may be concluded that although an elephant is fed hay, the quality of the hay itself is of considerable significance. Yet this fact is rarely taken into consideration. Hay is purchased on tour, and the elephant man has to take whatever is furnished him, hoping for the best. In any event the elephant itself is the loser.

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[1] Unpublished experiments on cows, carried out in cooperation with Professor E. G. Ritzman at the University of New Hampshire; cited briefly by F. S. Prince, P. T. Blood, and G. P. Percival, Univ. New Hampshire, Agric. Exper. Sta., Station Circular 41, May 1933, p. 4.

The practise of wintering live stock on scant rations is almost universal. Experiments have shown that domestic animals can be carried through the winter on an extraordinarily low nutritive plane without serious impairment to health, and that these animals will have perfect power to recuperate rapidly when pasturage or more liberal feeding is given in the spring. Consequently from the standpoint of the health of the animal itself, the normal reserve of fat in any animal allows for a great, temporary variability in the food supplies. Thus an elephant may exist for weeks, if not months, on low rations and draw meanwhile heavily upon its previously stored fat, and yet this would not seriously affect its health or power of recuperation. Hence any transitory change in the quality and amount of the hay fed to the elephant while on tour can play relatively little rôle in the ultimate physical condition of the animal, provided there is sufficient balancing of poor food material with good food material.

The Elephant's Teeth and Mastication

In our earliest studies on Jap it was observed that the degree of mastication was apparently small in proportion to what one would expect from the highly developed tooth structure. In the preparation of this report it became apparent from conversation with palæontologists that because of the significance of the structure of the elephant's tooth in terms of its evolutionary history, a closer study of its eating processes should be made.

Observations undertaken specifically for this purpose were confined in large part to those upon the two elephants at the Franklin Park Zoo, and we are indebted to Director Harkins and Keepers Clark and Veasey for every courtesy in making these observations. A study of the eating processes of the elephant may consist of two separate types of observations, (1) regarding the movements of the jaws for a given amount of food and, indeed, foods of widely different character, and (2) regarding the degree to which pieces of rubber imbedded in bread and eaten by the elephant are damaged or marked by the teeth in the chewing process. Associated with this analysis was the simultaneous study of the length of time taken by these pieces of rubber to pass through the alimentary tract and be recovered in the feces. This latter study gave a hint as to the rate of passage of food through the alimentary tract. This particular feature will be discussed subsequently. (See page 189.) At this point we are primarily interested in the mechanics of eating. The elephants were fed entire loaves (about 570 grams each) of bread, in which were imbedded from five to ten pieces of rubber of distinctive shapes so as to be readily recognized if they appeared fairly intact in the feces. In general these pieces of rubber were approximately 10 cm. long and 4 cm. wide, cut out of automobile inner rubber tubing approximately 3 mm. thick, in the shape of diamonds and rectangles. In some experiments rubber bands a centimeter or more wide and 8 to 18 cm. long were administered.

Eating bread—The two elephants at the Franklin Park Zoo apparently had widely varying eating habits when eating bread, for by counting the number of jaw movements for each consecutive quarter or half minute and noting the time when the bread disappeared, it was found that one elephant, No. 3, required about 4½ minutes to swallow the loaf of bread, whereas the other elephant, No. 2, required more nearly one minute or a minute and a half. The number of jaw movements made by elephant No. 2 in 15 seconds, during the eating of four successive loaves of bread, were 10, 9, 9, and 6, respectively. In 30 seconds, during the eating of the first loaf, there were 17 jaw movements. The total time taken to eat each loaf of bread was, respectively, 48, 90, 54, and 96 seconds. The number of jaw movements made by elephant No. 3 in eating three successive loaves of bread were as follows:

Loaf No.	Number of jaw movements in							
	¼ min.	1 min.	1½ min.	2 min.	2½ min.	3 min.	3½ min.	4 min.
2	....	....	24	....	52	66	....	78
3	6	21	37	53	71	88	98	....
4	5	12	23	40	53	68	81	....

The total time taken by No. 3 to eat four successive loaves of bread was 4.8, 6.0, 4.5, and 3.5 minutes, respectively. Thus, so far as this soft food (an entire loaf, 570 grams, of bread) is concerned, the eating habits of these two elephants were widely different. Further observations on the chewing of bread by the elephant seemed to be necessary, on account of the wide difference between the two animals, Nos. 2 and 3. Engineer Ackerman fed the elephant Jap six loaves of bread at different times and noted the length of time before the bread disappeared from the mouth. The shortest time was 18 seconds, the longest 22 seconds, and the average time for the six loaves was 20 seconds. Similarly Mr. Larry Davis, associated with the Ringling herd in Florida, made recently the same test with ten elephants.

Each elephant was given the usual full loaf of unsliced bread, without the waxed paper wrapping, and the time was noted when the bread was swallowed and there was no visible portion of it in the mouth. The times were as follows:

Elephant No.	15	18	21	22	29	33	35	44	45	47
Seconds to swallow bread.....	38	85	60	34	65	55	20	20	67	22

These observations confirm the findings on elephant No. 2 and emphasize that No. 3 is an exception in eating bread very slowly.

Eating hay—When hay was given, the situation was much more nearly the same with the two elephants. An attempt was made to estimate the amount of hay taken up to the mouth by the trunk with each feeding. This was done in two ways: (1) By deliberately removing from the animal the small bunch of hay as it was taken up in the trunk, ready to be carried to the mouth, and (2) by trying to estimate by the eye the approximate mass of this hay. Obviously the hay was bulky and only approximate measurements were possible. The maximum length of a portion was approximately 16 inches and the length of the main mass about 12 inches. The circumference of the hay when rolled tightly was about 4 inches, and that of the loose hay when the elephant had it in the trunk about 6½ inches. The weight of this particular mass was 48 grams. A portion of hay representing that taken up in the trunk by the elephant had an over-all length of about 1 foot 10 inches and weighed about 110 gm. Another portion of hay taken away from one of the elephants weighed 58 gm., the average length being 17 inches. A third portion taken away from the other elephant had an average length of 1 foot; the circumference of this hay as held by the elephant was 8 inches and the weight 69 grams. Still another portion weighed 90 grams, the average length being 15 inches and the circumference 7 inches. Approximately, therefore, these elephants picked up about 80 grams with each movement of the trunk to the mouth.

The measurement of the number of hay portions carried to the mouth in 3 minutes, together with the actual number of jaw movements in 3 minutes by both elephants, is recorded in table 22A. With No. 2 the actual number of hay portions varied from 4 to 8, but the total number of jaw movements in 3 minutes was reasonably uniform at about 75. With No. 3, the number of hay portions was from 4 to 6, but the jaw movements in 3 minutes were essentially the same as with No. 2, that is, about 75. On the average, each of the two elephants in 3 minutes took to its mouth about 5 portions of hay weighing approximately 80 grams each or essentially 1 pound, and the preparation given to this amount of hay in 3 minutes was the equivalent of approximately 75 jaw movements. This number of jaw movements in 3 minutes occupied in eating hay is almost exactly that used by one of the animals, No. 3, in chewing a loaf of bread, but No. 2 disposed of her bread in more nearly a dozen movements.

Type of jaw movement—The only motions of the jaws that we were able to observe were vertical. Toward the end of the period of chewing there was a small forward motion, when the lower jaw apparently slid forward a small amount. There was no indication of any lateral movement.

It is impossible to detect with these animals a swallowing motion. This is true as well when they are eating hay or bread as when they are drinking water.

The relatively rapid swallowing, without chewing, of bread may be criticized on the ground that this is a wholly unusual food material for the elephant. On the other hand, bread, with its approximately 40 per cent water, demands relatively little insalivation and, having four times the amount of water present in ordinary hay, tends to approximate the succulent feed of the elephant in the wild.

The tongue apparently plays a great rôle in the transport of food, but there was nothing in our close observations of the jaw movements to suggest any use of the highly developed teeth as grinding apparatus.

Use of teeth as indicated by marks on rubber fed—The second criterion of jaw activity and tooth use was the examination of the various pieces of rubber fed to these elephants in their loaves of bread, and subsequently recovered in the feces. In the case of Jap (see page 191) many of the pieces of rubber fed to her came through unaffected or in no wise damaged. On the other hand, a few pieces came through very much chopped up and some

TABLE 22A—*Motion study of elephants when eating hay*

Time in minutes	Elephant No. 2								Elephant No. 3					
	Dec. 12 (8.35 a.m.)		Dec. 12 (8.47 a.m.)		Dec. 12 (4.15 p.m.)		Dec. 13 (8.20 a.m.)		Dec. 12 (8.40 a.m.)		Dec. 12 (8.51 a.m.)		Dec. 12 (4.19 p.m.)	
	Mouthfuls	Jaw movements	Mouthfuls	Jaw movements	Mouthfuls	Jaw movements	Mouthfuls	Jaw movements	Mouthfuls	Jaw movements	Mouthfuls	Jaw movements	Mouthfuls	Jaw movements
0	1	....	1	....	1	....	1	....	1	....	1	....	1	....
.25	....	8	2	5	....	6	....	6	....	8	....	6	....	8
.50	1	14	....	10	....	13	....	10	....	13	....	13	1	12
.75	....	18	....	15	....	20	1	16	1	19	1	18	1	18
1.00	1	24	1	21	1	24	....	23	....	25	1	23	....	25
1.25	....	30	....	26	....	33	....	29	....	33	....	30	....	31
1.50	1	36	1	32	....	41	....	36	1	39	....	36	....	38
1.75	1	42	....	37	....	48	....	....	....	45	....	41	....	45
2.00	....	50	1	42	1	54	1	48	1	52	....	46	....	50
2.25	1	57	....	48	....	....	....	....	....	58	1	51	....	57
2.50	....	63	....	54	....	68	....	60	1	65	....	57	1	63
2.75	1	69	1	60	....	....	....	64	....	70	....	63	....	69
3.00	1	74	....	66	1	86	1	70	1	76	....	69	....	79
Total mouthfuls	8	....	7	....	4	....	4	....	6	....	4	....	4	....

were never recovered, which speaks, of course, for considerable tooth action. To the two Franklin Park elephants rubber was fed in loaves of bread at various times, for two purposes: (1) To note the degree to which the tooth action would be shown on the pieces of rubber, and (2) to study the time element for the rubber to pass through the intestinal tract. The elephants were fed their bread containing pieces of rubber between 2.30 and 3.00 p.m. on one afternoon. Up until 4.30 p.m. the next day, that is, more than 25 hours after feeding, no traces of rubber were present in the feces. Confirmatory evidence, however, of the poor comminution in the case of at least one of these elephants was shown by the fact that in the feces of No. 2 there were several portions of red beets about the size of half a golf ball, or even larger, which were in good condition, that is, they had not been chewed or crushed. At least three such pieces were found in the feces of this animal.

The precise time at which the rubber appeared in the feces could not be controlled, as we were not allowed to have an assistant with the animals after 4.30 p.m., but with the help of the keepers an estimate was made that the rubber appeared substantially at the time noted with Jap. The complete collection of the rubber pieces fed was imperfect, inasmuch as we could not personally examine all the feces, but approximately half of the rubber fed was recovered and probably many more pieces were actually present in the feces but undetected, for the feces were not critically examined. Of far greater importance than the time element, however, was the degree to which this rubber was marked by the teeth. With these animals, as with Jap, by far the larger number of the pieces were not altered or cut so as to change their shape. One of the pieces with each elephant was cut noticeably, but aside from this there was no evidence of the animal's teeth having injured the rubber measurably.

The evidence, therefore, in this series of tests is to the effect that the chewing process of the elephant is not sufficiently extensive, in spite of the highly developed chewing surfaces of the teeth, to mark, much less destroy, a large proportion of the number of rubber pieces fed to her. It may be argued that rubber is a poor substance to be used in such a test, but it should be recalled that the study was made primarily to indicate the time in which the food would pass through the intestinal tract, and only secondarily for studying the tooth action. The elephants did not belong to us, but we were able, from our previous experience with the elephant Jap (see page 190), to assure the keepers that feeding rubber would not be harmful, and thus we obtained permission to do so.

We believe, however, that the obvious physical characteristics of the elephant dung (consisting almost exclusively of pieces of hay 5 to 15 cm. long), the appearance of relatively large pieces of unaltered beets in the feces of one of the elephants, and the fact that the rubber for the most part showed no teeth marks are all indications of a very poor comminution. Examination of the mechanical structure of a bolus of feces indicates that it is composed of a series of interlocking or interlacing pieces of fiber. Were this material finely comminuted, these boluses could not possibly hold their shape. It is true that the finely comminuted material in the pellets or small bits of dung from the sheep fall to the ground unbroken. Since their diameter is about 7 mm., this is not surprising. But the fact that a bolus of elephant feces of 140 mm. diameter will fall a distance of 2 meters and not break is of itself proof of the highly interlacing internal structure of the long, fibrous fecal material. The horse has much poorer comminution than the sheep, and the degree of coarseness of its feces, although not comparable, would at least approach that of elephant feces. The balls of horse feces, about 30 mm. in diameter, drop from a height of a meter and a half and are not broken. These without doubt are held together by the fibrous structure of the feces, and gravity can not flatten them as they strike the ground, in contrast to the finely comminuted, soft feces of the cow or steer.

This feature of the structure of the bolus of elephant feces leads us to believe that even the feces of elephants in the wild in Africa and India, that are found by hunters to retain still this ball-like form, must of necessity be composed of a large mass of undigested, fibrous material, which of itself is proof of poor comminution even when the elephants have access to food not dictated by the economics or whims of man.

We are indebted to Dr. W. M. Mann of the National Zoological Park, at Washington, D. C., for the information that, according to his own personal observations of the African elephant in the wild, the feces are made up in large part of pieces of undigested grass, twigs, and stems of leaves. This speaks again for the extremely poor comminution of food by the elephant.

Two studies of the jaw movements of Herbivora that may be compared with our study on the elephant may here be cited. The early observations of Colin[1] showed that a horse required 1¼ hours to eat 2 kg. of dried hay, of which he made from 60 to 66 boluses. In this process the chewing movements were approximately at the rate of 70 to 80 per minute, and the hay was eaten at the rate of about 30 grams per minute. In the case of the elephant approximately 75 jaw movements in 3 minutes (25 jaw movements per minute) accompanied the mastication of from four to eight portions of hay weighing approximately 80 grams each. If a direct comparison with the horse is justifiable, 30 grams of hay would call for about 6 jaw movements of the elephant as compared with 75 jaw movements by the horse for the same mass of hay. Obviously the degree of comminution of the hay by the horse must have been very much greater. With the ruminant (the cow) the eating process is complicated, inasmuch as the first mastication is followed by the longer rumination or second degree of chewing, and the picture is by no means so clear as with the horse and the elephant.

The most elaborate data on this subject are a series of observations carried out under the writer's direction by Fuller[2] of the University of New Hampshire, in which it was noted that when cows were eating hay (no estimate was made of the amount of hay eaten at the time), they made about 78 jaw movements per minute. The second process of comminution, that is, ruminating, is made at a much more leisurely pace and may occupy many hours, but even a cow chews her food at the moment of its intake much longer proportionately than does the elephant.

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[1] Colin, G., *Traité de physiologie comparée des animaux*, Paris, 1886, 3d ed., I, p. 645.

[2] Fuller, J. M., Univ. New Hampshire, Agric. Exper. Sta., Tech. Bull. 35, 1928.

Palæontologists lay great stress upon the character, area, convolution, and configuration of the grinding teeth of the Proboscidea.[1] Perhaps no one other anatomical factor has been given more attention, particularly in recent years. In view of the poor comminution of hay and the low apparent digestibility of hay by the elephant, one wonders how the teeth of this animal can play any great rôle in its economic utilizaton of food. Indeed, judging from these two facts alone, one could assume that the teeth play a small rôle in the digestive processes. To be sure, these observations have been made upon the elephant in captivity. What rôle the grinders play with the wild elephant feeding in the African forest on leaves and twigs and in the forests of India on bamboo shoots and some succulent or semi-succulent material can not be inferred from these studies. Certainly, however, in captivity the elephant fed dried grasses, in large part hay, thrives well even with poor comminution of food, and gains in weight. At the rate at which the hay is swallowed by the elephant it hardly seems possible that food boluses could be formed, and apparently there is no regurgitation in the sense of rumination.

The progressive development of strong transverse ridges on the teeth of Tertiary Proboscidea is interpreted by palæontologists as due to their feeding habits. Not only the configuration of the molar teeth but their renewal from behind, both in fossil and modern elephants, are considered an indication of their importance as grinding structures over tens of millions of years. In view of the poor comminution of hay and the low apparent digestibility of hay by the modern elephant, the question may well be raised as to whether its feeding habits, or in any case its methods of chewing, have not been profoundly altered since the earlier development of proboscidean tooth characters in the Tertiary period.

DRINKING WATER

As with all warm-blooded animals, a liberal supply of drinking water is absolutely essential to the normal health of the elephant. The enormous amounts of water consumed by a herd of elephants call for a liberal supply. Without doubt elephants in circus herds are given much more care than those in India, where often muddy water is the only water available. The amounts consumed are in the order of 35 to 50 gallons of water per day for an ordinary sized elephant. The Ringling herd are watered twice a day. Three large galvanized iron tubs are first filled wth water. Then usually five or six elephants are brought to the tubs, and they immediately begin to draw upon the water, sucking it into their trunks. Meanwhile a heavy stream of water, with a hose having a nozzle of 20 mm. diameter, is playing continually into the tubs, and it is a fact that the five elephants have in a very few moments taken all the water in the tubs and are taking the water from the hose as fast as it is delivered. The large elephants in the Downie herd are reported to drink about 35 gallons each per day.

The peculiar method of drinking followed by the elephant, that is, drawing a lot of water up into the trunk and then forcing it in a jet into the throat, was studied both in Florida and with the Franklin Park animals.

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[1] For an interesting discussion of the teeth of the Indian elephant see C. Röse, Schwalbe's Morphologische Arbeiten, Jena, 1894, 3, p. 173.

In Florida with several elephants whose trunks were partly paralyzed and hence could not be placed deep into the throat, it was noted that the jet of water blown out was passed directly into the mouth. No swallowing movement could be seen from the outside, and there was no cessation of the completion of the discharge from the trunk, a jet of water approximately 1½ inches in diameter being thrown into the throat. The amount of water taken with each trunkful and the time for the entire cycle required for filling the trunk with water and discharging it into the throat were studied at Franklin Park by having the water brought to the elephants in pails which had previously been weighed full of water. Each elephant put her trunk into the pail, filled the trunk with water, and discharged it into the mouth. The pail and the water left were weighed after each trunkful had been taken. The weights of water sucked up by each elephant in successive trunkfuls were as follows:

	No. 2 kg.	No. 3 kg.
	7.05	8.85
	5.65	5.00
	5.70	3.40
	6.85	5.30
	6.80	5.10
	6.85	5.05
	7.40	4.90
		4.80
		4.80
		4.35
		4.80
		4.05
		3.80
Avg.	6.61	4.59

On the average, No. 2 discharged into the mouth, after each trunkful was taken, 6.61 kg. of water; and No. 3 discharged 4.59 kg. The entire drinking cycle, that is, taking the water, raising the trunk to the mouth, and discharging the water down the throat, was approximately 0.06 minute (4 seconds).

Jap received water usually twice a day, in the morning and in the evening just before being fed, drinking about 40 gallons per day. Sometimes larger amounts than this were drunk, as shown by the data in table 23, in which are recorded the temperatures and the amounts of water drunk by the animal during the period from April 2 to 11. It is the custom of many circuses and shows to give animals water at a moderately warm temperature, not cold. Jap preferred water fairly hot, almost too hot for comfortable drinking by humans. However, most of the time at Campgaw she was given water directly from the faucet at a temperature of not far from 8° to 10° C. A galvanized iron tub was filled to within two or three centimeters of the top and carried by two men to the barn, or Jap came out to the tub. She drank the water by the usual method of drawing it up in the trunk and squirting it into the mouth. During the 9-day period from April 2 to 11 she drank, on the average, 139 kg. (about 35 gallons) of water per day. Since the water-free substance in the hay consumed daily amounted to 46 kg., Jap's daily water intake was 3.0 kg. per kilogram of dry matter in feed. This is lower than the 4.0 kg. assumed by Kellner[1] for cattle on full rations, but is more in accord with values found with steers.[2]

Through the kindness of Professor Henry C. Sherman, of the Department of Chemistry at Columbia University, New York City, we were put in touch with Mr. Amos E. Light of that same department, who cooperated in making an analysis of a sample of Jap's drinking water sent to him directly from Campgaw. The special object of this analysis was to determine whether, since salt was not fed to Jap, the drinking water contained any appreciable amount of solids to compensate for this lack of salt in the diet. We are indebted to Mr. Light for his courtesy in making this analysis, the results of which are as follows:

TABLE 23—*Amount and temperature of water drunk by the elephant Jap*

Date and time	Temperature of water	Amount drunk at one time	Total amount drunk per day
1935	°*C.*	*kg.*	*kg.*
Apr. 3			
7.55– 8.03 a.m.		82.70	
12.55 p.m.		60.00	142.70
Apr. 4			
9.17– 9.24 a.m.		86.52	
4.09– 4.15 p.m.		64.36	
6.30 p.m.		29.42	180.30
Apr. 5			
9.26 a.m.	8.9	41.73	
5.16 p.m.	8.7	25.27	67.00
Apr. 6			
7.50 a.m.	8.2	84.50	
11.24 a.m.	8.1	39.03	
6.45– 7.15 p.m.	8.2	76.74	200.27
Apr. 7			
7.06– 7.27 a.m.	8.2	76.62	
11.40–11.53 a.m.	7.5	49.88	
12 noon	7.5	14.38[1]	
10.55 p.m.	9.0	36.96	177.84
Apr. 8			
8.40 a.m.	8.9	39.32	
6.40 p.m.	10.6	69.11	108.43
Apr. 9			
1.30– 1.34 p.m.	10.0	112.12	
6 p. m.	10.1	41.50	153.62
Apr. 10			
9.15 a.m.	9.4	85.96	
ca. 6 p.m.	12.1	16.71	
8.32 p.m.	10.2	29.85	132.52
Apr. 11			
1.03 p.m.	10.0	23.54	
4.44– 4.48 p.m.	10.0	67.37	90.91

[1] Given at noon; did not drink until later.

Total solids	119 parts per million
Total mineral residue	88 parts per million
Total chlorine	6 to 7 parts per million

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[1] Kellner, O., *Die Ernährung der landwirtschaftlichen Nutztiere,* 9th ed., Berlin, 1920, p. 185.

[2] Benedict, F. G., and E. G. Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 116.

Mr. Light reports that the chlorine is normal for the locality at Campgaw, but that the results for mineral residue and total solids are possibly low. The total solids in other New Jersey water samples approach 200 parts per million. Thus it is clear that no great amount of solids were obtained by Jap in her drinking water. Since she drank on the average about 140 kg. per day (see table 23), she would obtain from this source about 17 grams of total solids per day and about 1 gram of total chlorine (1.6 gm. of sodium chloride), wholly insignificant amounts. (For further discussion of this point see page 229.)

One feature with regard to the drinking water of elephants has been strongly emphasized in our experience, that is, that elephants prefer water of rather a warm temperature. This was clearly brought out by the custom frequently in vogue of heating Jap's water when she was in a stable in New York and her evident delight in taking water that would be considered by the ordinary person very warm if not, indeed, hot. It was also frequently observed that Jap, when taking a large volume of water (20 to 25 gallons at a watering) at a temperature not far from 8° C., was seriously chilled. It would appear, therefore, a good practise, especially in winter, to give elephants water fairly warm.

At this point it may be worth while noting that the commonly reported ability of elephants to draw rather considerable quantities of water from their mouth cavities, at times, finds no substantiation in Doherty's experience. Slight amounts of mucus may be withdrawn and blown out as spray over the head or the body, and there is always condensed water in the trunk of the elephant from the blast of warm, saturated air from the lungs. This, when a sudden blast is given, gives the impression of spraying water about, but that any amount of water (frequently stated to be as much as a gallon or more) can be drawn from the throat of the elephant has never been observed in the experiences of any of the elephant men with whom we have been in contact.

FECES

The feces of the elephant are of physiological interest from several standpoints. In the first place, the mechanics of defecation should be studied, to note the frequency of defecation, the number of boluses of feces passed at each defecation, and the size of the boluses. Secondly, the chemical composition is of interest, that is, the percentage of water, dry matter, crude fiber, protein, fat, and ash in the feces. Macroscopic and microscopic examinations of the feces are also of importance, to note whether they contain undigested material and parasites. Finally, the rate of passage of food through the intestinal tract can be studied by means of the feces. With Jap the examination of the feces from these several standpoints was reasonably complete, but again, because of unwillingness to base the entire discussion of these factors upon observations on only one animal, numerous supplementary observations were made on the feces of the several elephant herds with which contacts were made.

Method of collecting feces—By placing a canvas under the hind quarters of Jap, it was possible to obtain uncontaminated samples of feces, and since an observer was continually on hand, the samples were obtained before they were crushed by Jap's lying or stepping on them. Complete collections were obtained only from Jap. Individual samples were collected from the herds of elephants by various methods, more frequently by having the balls fall upon the ground and then collecting them individually. With the Barnes herd attempts were made to collect them as they left the anus, in large wire-mesh scoops, one for each ball.

Character of feces—The most striking characteristic of the elephant's feces is that they are made up almost exclusively of unattacked or but slightly attacked hay. Thus they give the impression of a mass of chopped hay, most of the pieces of hay being approximately 25 mm. and at times 150 mm. long. This was particularly true of the feces of Jap, who was fed hay only. The other elephants, which were fed hay, bran, and oats, had feces not differing widely from those of Jap, except that occasionally undigested particles of oats and more finely comminuted, softer material that might be bran residues were visible in their feces. The balls of feces from these elephants were a little less hard than those of Jap. Her balls usually would not break open when they fell to the floor, but the balls passed by the other elephants frequently, though not usually, broke on reaching the floor. There was no particularly marked or offensive odor about any of the feces. In color they were darker on the outside, where they had been in contact longer with the mucous lining of the intestines, and much lighter inside. Their consistency was not far from that of horse feces, but the fecal matter was not so finely comminuted or soft as that of the cow and the steer or, indeed, the horse.

Parasites—In the examination of the feces, particular attention was given to those portions that came in contact with the intestinal tract, that is, the outer portion of the bolus, with the idea that any parasites attached to the walls of the intestines might be carried out of the intestinal tract along with the feces. Under no conditions, however, were visible parasites noted. Microscopic examinations made in many cases also showed no parasites. It would appear that the elephant in captivity has been practically freed from parasites. This may be due in part to the diet, that is, to the fact that there is little opportunity for getting parasitic organisms in the hay and grain as fed, or it may be due to the trained vigilance of the various keepers, who are always on the lookout for the possibility of parasites and apply suitable remedies to remove them. Doherty states that all the Ringling elephants at times had a mild infestation of worms in the feces, and one always has to be on the watch for them. It is necessary to give the elephant a vermifuge, probably chiefly turpentine, although many other well-known veterinary medicaments are used. Doherty emphasized the difficulty of persuading the elephants to take this and said he usually gave it in potatoes. Ordinarily when other medicines are given, a syringe is used and put well down in the mouth. In the numerous specimens of feces examined in this study, both macroscopically and microscopically, no parasites were found. In this respect the condition of the captive elephant is in striking contrast to the reported condition of the wild elephant, which is said to be heavily infested with parasites.[1]

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[1] Kofoid, C. A., Proc. Nat. Acad. Sci., 1935, 21, p. 501.

TABLE 24—*Weights of each defecation and average weight per bolus of feces passed by the elephant Jap*

Date and time	Number of boluses	Weight of defe-cation	Average weight per bolus
1935		*kg.*	*kg.*
Apr. 3			
12.10 a.m.....	6	6.79	1.13
1.14 a.m.....	7	6.28	.90
2.25 a.m.....	6	5.82	.97
2.55 a.m.....	7	5.80	.83
4.18 a.m.....	7	5.90	.84
5.58 a.m.....	6	5.84	.97
6.44 a.m.....	8	6.17	.77
7.36 a.m.....	6	5.35	.89
8.11 a.m.....	5	4.62	.92
9.15 a.m.....	6	5.19	.87
10.25 a.m.....	4	5.09	1.27
11.22 a.m.....	5	7.02	1.40
12.40 p.m.....	5	5.31	1.06
1.15 p.m.....	4	5.98	1.50
2.10 p.m.....	3	2.68	.89
3.00 p.m.....	3	5.97	1.99
4.15 p.m.....	5	5.78	1.16
5.20 p.m.....	4	4.51	1.13
6.05 p.m.....	5	6.28	1.26
7.38 p.m....	6	6.51	1.09
8.35 p.m.....	7	7.14	1.02
9.54 p.m.....	8	6.15	.77
11.06 p.m.....	6	6.18	1.03
11.55 p.m.....	4	5.58	1.40
Apr. 4			
12.52 a.m.....	5[1]	5.60	1.12
1935		*kg.*	*kg.*
Apr. 6			
12.09 a.m.....	6	4.90	.82
1.10 a.m.....	4	5.04	1.26
2.25 a.m.....	(3)	4.12	1.37
3.31 a.m.....	4	5.34	1.34
5.46 a.m.....	6	6.70	1.12
6.43 a.m.....	6	6.60	1.10
8.05 a.m.....	4	3.25	.81
8.40 a.m.....	4	4.04	1.01
10.36 a.m.....	7	6.25	.89
11.36 a.m.....	5	4.80	.96
12.52 p.m.....	6	5.50	.92
1.54 p.m.....	4	3.91	.98
2.18 p.m.....	4	4.96	1.24
3.34 p.m.....	5	5.11	1.02
4.36 p.m.....	5	6.42	1.28
5.24 p.m.....	5	5.20	1.04
6.30 p.m.....	8	10.97	1.37
8.19 p.m.....	4	4.16	1.04
9.12 p.m.....	5	4.86	.97
10.07 p.m.....	4	5.37	1.34
10.50 p.m.....	5	7.52	1.50
11.52 p.m.....	(4)	4.71	1.18
Apr. 7			
12.38 a.m.....	7	6.67	.95
1.36 a.m.....	9	10.43	1.16
3.50 a.m.....	10	9.27	.93
1935		*kg.*	*kg.*
Apr. 8 (Cont'd.)			
8.00 p.m.....	5	4.70	.94
9.14 p.m.....	5	6.02	1.20
11.18 p.m.....	8	4.91	.61
11.45 p.m.....	4	4.36	1.09
Apr. 9			
1.33 a.m.....	6	5.59	.93
2.50 a.m.....	5	4.58	.92
4.40 a.m.....	11[1]	8.75	.80
6.27 a.m.....	4	4.76	1.19
7.50 a.m.....	5	5.38	1.08
9.26 a.m.....	4	4.11	1.03
11.36 a.m.....	5	5.90	1.18
2.45 p.m.....	(7)	5.58	.80
3.53 p.m.....	7	5.34	.76
4.55 p.m.....	5	3.44	.69
5.45 p.m.....	5	5.52	1.10
6.32 p.m.....	4	4.75	1.19
7.21 p.m.....	8	7.30	.91
8.54 p.m.....	6	4.94	.82
10.05 p.m.....	6	6.15	1.03
11.02 p.m.....	5	5.76	1.15
Apr. 10			
12.19 a.m.....	5	6.73	1.35
12.52 a.m.....	5	5.22	1.04
1.59 a.m.....	5	5.63	1.13
3.05 a.m.....	4	5.23	1.31

2.21 a.m.....	4	5.79	1.45	5.35 a.m.....	5	5.58	1.12	4.45 a.m.....	4	5.63	1.41
3.20 a.m.....	4	4.90	1.23	6.55 a.m.....	5	4.87	.97	5.22 a.m.....	7[1]	5.12	.73
4.17 a.m.....	5[1]	5.33	1.07	7.12 a.m.....	5	5.34	1.07	6.41 a.m.....	5	4.31	.86
6.00 a.m.....	3	4.12	1.37	8.00 a.m.....	5	3.99	.80	7.16 a.m.....	5	4.75	.95
7.02 a.m.....	5	5.90	1.18	8.58 a.m.....	4	5.72	1.43	9.15 a.m.....	7	9.08	1.30
8.49 a.m.....	6	5.75	.96	10.00 a.m.....	5	4.57	.91	11.15 a.m.....	4	3.30	.83
9.46 a.m.....	6	5.21	.87	10.35 a.m.....	4	6.27	1.57	12.15 p.m.....	4	5.57	1.39
11.10 a.m.....	7	5.77	.82	11.42 a.m.....	5	5.63	1.13	1.20 p.m.....	5	5.71	1.14
12.46 p.m.....	6	5.69	.95	12.42 p.m.....	5	6.00	1.20	2.15 p.m.....	6	6.16	1.03
2.14 p.m.....	6	4.90	.82	1.35 p.m.....	4	5.65	1.41	3.35 p.m.....	5	6.66	1.33
3.36 p.m.....	6	5.58	.93	2.47 p.m.....	4	5.50	1.38	4.36 p.m.....	4	5.65	1.41
4.44 p.m.....	4	4.52	1.13	3.21 p.m.....	4	....	....	6.47 p.m.....	6	6.42	1.07
5.39 p.m.....	4	4.70	1.18	4.35 p.m.....	4	6.16	1.54	6.55 p.m.....	4	6.84	1.71
6.46 p.m.....	5	5.85	1.17	5.20 p.m.....	4	5.30	1.33	8.38 p.m.....	5	6.78	1.36
7.59 p.m.....	5	6.40	1.28	6.10 p.m.....	5	6.62	1.32	10.08 p.m.....	4	4.83	1.21
9.10 p.m.....	4	5.53	1.38	7.22 p.m.....	9	10.95	1.22	10.45 p.m.....	(4)	4.46	1.12
10.09 p.m.....	5	5.27	1.05	9.03 p.m.....	6	10.81	1.80	Apr. 11			
11.15 p.m.....	6	5.70	.95	10.46 p.m.....	6	6.20	1.03	12.50 a.m.....	6	7.04	1.17
Apr. 5				11.43 p.m.....	6	5.52	.92	2.25 a.m.....	5	5.09	1.02
12.17 a.m.....	4	4.48	1.12	Apr. 8				4.00 a.m.....	(4)[1]	4.83	1.21
1.18 a.m.....	5	5.91	1.18	12.30 a.m.....	7	10.25	1.46	6.10 a.m.....	5	5.27	1.05
2.26 a.m.....	5	5.25	1.05	2.20 a.m.....	6[1]	6.33	1.06	7.44 a.m.....	6	6.22	1.04
3.42 a.m.....	5[1]	5.81	1.16	3.50 a.m.....	5	5.40	1.08	9.39 a.m.....	5	6.12	1.22
5.08 a.m.....	5	5.20	1.04	5.28 a.m.....	5	8.58	1.72	1.00 p.m.....	6	9.47	1.58
6.05 a.m.....	5	4.43	.89	6.54 a.m.....	11	10.65	.97	3.30 p.m.....	5	5.99	1.20
7.31 a.m.....	6	4.76	.79	8.46 a.m.....	4	5.71	1.43	5.00 p.m.....	6	5.16	.86
8.53 a.m.....	6	5.25	.88	9.36 a.m.....	6	6.24	1.04	6.21 p.m.....	5	5.44	1.09
10.42 a.m.....	4	4.80	1.20	10.55 a.m.....	5	5.21	1.04	7.40 p.m.....	7	7.40	1.06
12.40 p.m.....	4	5.18	1.30	12.10 p.m.....	6	5.67	.95	8.50 p.m.....	5	4.75	.95
3.41 p.m.....	6	6.75	1.13	1.03 p.m.....	6	5.91	.99	10.02 p.m.....	(5)	6.04	1.21
6.40 p.m.....	(6)	6.21	1.04	2.25 p.m.....	5	5.14	1.03	11.32 p.m.....	5	6.36	1.27
7.59 p.m.....	7	6.79	.97	3.40 p.m.....	6	4.78	.80				
9.53 p.m.....	8	7.18	.90	4.59 p.m.....	6	6.05	1.01				
10.42 p.m.....	6	5.79	.97	6.50 p.m.....	6	5.88	.98				

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[1] Jap was lying when feces were passed; in all other instances she was standing.

Benzidine test—One of the assistants (Mrs. H. E. Mayo) in the laboratory of Dr. H. E. Thompson at the Eastern Maine General Hospital at Bangor, Maine, had the initiative to make the benzidine test on samples of elephant feces. She reported that the benzidine test was positive on all three samples of feces sent to Dr. Thompson from the Ringling herd. This test was then carried out under the expert guidance of Dr. Alexander Marble at the New England Deaconess Hospital, Boston, Massachusetts, on nine specimens of feces from the Downie herd. In the clinical laboratories the test for occult blood in feces is made by adding a few drops of a solution of benzidine in glacial acetic acid and a few drops of 3 per cent hydrogen peroxide to a small bit of feces which has been smeared on a watch-glass. If a greenish-blue color is produced, this is regarded as strongly suggesting the presence of blood pigments. A refinement of this method is as follows:

A sample of feces is first emulsified with distilled water, the fat is then extracted with ether and the ether layer discarded. The water emulsion is next acidified with glacial acetic acid and again shaken with ether to extract the blood pigments in the acidified emulsion. A portion of the ether extract is then underlaid with a freshly prepared solution of benzidine in glacial acetic acid to which has been added an equal quantity of 3 per cent hydrogen peroxide. If a bluish-green ring is obtained, this is accepted as suggesting the presence of blood.

When this procedure was used with the feces samples from the Downie herd, the test was positive in all cases, thus fully confirming Mrs. Mayo's wholly unexpected finding. Further tests were made on the feces of the two elephants at Franklin Park in Boston and on the dried samples of Jap's feces. Again in all instances the tests were positive, although with varying degrees of intensity. The large amount of unattacked hay in the feces, with the heavy proportion of fibrous material, suggested that this unusually irritating mass might conceivably lacerate continuously the one hundred or more feet of intestinal tract and thus logically account for the apparent presence of blood in the feces, as shown by this test. On the theory that the coarse fiber of the poorly comminuted hay might have resulted in excessive laceration of the mucous lining of the elephant's intestines, it was argued that if the test is found positive with the elephant it should disappear in the case of those Herbivora that chew their food more finely. Consequently tests were made on feces from lambs, several horses, and cows (obtained through the courtesy of Professor E. G. Ritzman of the University of New Hampshire), on the feces of the hippopotamus at Franklin Park, and on the feces of rabbits from the colony of Professor W. E. Castle, of Bussey Institution, Harvard University. The tests were positive in all cases, but there was no suggestion of blood being present in any greater degree in the feces of any particular animal. Attempts to identify red-blood corpuscles under the microscope were invariably unsatisfactory. But microscopic examination would not necessarily show red-blood corpuscles, due to the fact that a hemorrhage or other source of blood might occur far enough up in the intestinal tract so that when the feces were excreted the red-blood corpuscles would have been already hemolyzed. Thus it would appear that the benzidine test may be supersensitive and not actually positive for elephants or the other Herbivora.

Frequency of defecation—In March 1935 scattered observations on Jap on five days indicated that from three to seven boluses were passed with each defecation. In April more complete records were made with Jap on nine consecutive days (April 2 to 11) regarding the times each day when feces were passed, the number of balls in each discharge, the total weight of each defecation, and the average weight per individual bolus. The data are summarized in tables 24 and 25. At times it was somewhat difficult to count precisely the number of boluses of feces discharged. In those few instances the number of boluses has been calculated from the total weight of the defecation and the average weight per bolus, as indicated by the average of all observations. These estimates, which have been enclosed in parentheses in table 24, are in all probability not far from correct. Jap defecated about once every hour. On the average, she defecated nineteen times and produced a total of 101 balls of feces in 24 hours. The total number of defecations per day varied from a minimum of 14 to a maximum of 24, and the total number of boluses per day from 75 to 133. At each defecation from 3 to 11 boluses were passed, and 5 boluses as the average. The frequency of defecation must be closely correlated with the eating habits of the animal and the character of the ration. In the case of Jap the ration was almost exclusively hay. Hence this time relationship in defecation deals with the feces resulting from the ingestion of hay only.

TABLE 25—*Frequency and weights of defecations—elephant Jap*

Date	Time	Defecations per day	Boluses per day	Number of boluses per defecation		Daily weight of fresh feces	Average weight per bolus
				Minimum	Maximum		
1935						*kg.*	*kg.*
Apr. 3	12.10 a.m.–11.55 p.m.	24	133	3	8	137.94	1.04
Apr. 4	12.52 a.m.–11.15 p.m.	19	96	3	7	102.51	1.07
Apr. 5	12.17 a.m.–10.42 p.m.	15	82	4	8	83.79	1.02
Apr. 6	12.09 a.m.–11.52 p.m.	22	108	3	8	119.73	1.11
Apr. 7	12.38 a.m.–11.43 p.m.	22	121	4	10	137.05	1.13
Apr. 8	12.30 a.m.–11.45 p.m.	18	106	4	11	111.79	1.05
Apr. 9	1.33 a.m.–11.02 p.m.	16	93	4	11	87.85	.94
Apr. 10	12.19 a.m.–10.45 p.m.	20	98	4	7	114.08	1.16
Apr. 11	12.50 a.m.–11.32 p.m.	14	75	4	7	85.18	1.14

Weights of individual and total daily defecations—The individual defecations varied in weight from 2.68 to 10.97 kg. and averaged 5.80 kg. The total daily weight of fresh feces varied from 138 kg. (a total of 24 defecations and 133 boluses) on April 3 to 84 kg. (a total of 15 defecations and 82 boluses) on April 5. There was considerable variability in the total daily weights of feces. Whether this variability was due to irregularity in discharge or whether it represents a true difference in formation of feces is not obvious from an inspection of the daily food intake. (See table 22.) The hay intake on these nine days varied greatly, and although it is true that on two of the three days when the maximum amounts of hay were eaten (that is, over 60 kg. on April 3, 7, and 9) maximum amounts of feces were discharged, nevertheless the minimum fecal discharge did not coincide with the lowest food intake. This indicates that there can be considerable irregularity in the passing of feces independent in large part of the irregularity in the food intake.

Weights of individual boluses—From the weight of each defecation and the number of balls of feces in each defecation have been calculated the average weights per individual bolus. The average minimum weight was 0.61 and the average maximum weight 1.99 kg. This average maximum weight represents three boluses passed at 3 p.m. on April 3. Prior to this study in April a bolus had been weighed in March amounting to 1.85 kg. Thus a 4000-kg. elephant can discharge a ball of feces weighing essentially 2 kg. Further evidence with regard to the weight of individual boluses was obtained by weighing a number of the balls in the case of the Barnes herd. Twelve individual balls from seven elephants in this herd varied in weight from 590 grams to 1.63 kg. The average weight of a ball of feces, in general, may be calculated from the results of the nine days' observations on Jap. Thus, during these nine days, 912 boluses were passed having a total weight of 979.92 kg. or, on the average, 1.07 kg. per bolus. On two occasions, March 12 and 13, when Jap was inside the respiration chamber for a period of from four to five hours, the entire feces passed during the experiment were collected and weighed. The total amount discharged on each occasion filled a large-sized washtub and amounted to 21.4 and 27.6 kg., respectively. Since the number of balls in the first instance was about twenty and in the second twenty-eight, the average weight per bolus in March was not far from 1 kg. Hence the average weight of the feces bolus in the first Campgaw study with Jap agreed closely with the average weight in the second study, and it can be assumed that the food levels were not greatly different at these two times.

Measurements of individual boluses—A ball of elephant feces is shaped somewhat like a truncated cone, the diameter of one end usually being smaller than that of the other. In a typical case of a bolus passed by Jap, weighing 1.26 kg., the diameter of the smaller end was 121 mm., that of the larger end 140 mm., and the length 165 mm. All the boluses of Jap that were measured had this general shape, with the smaller end about 114 to 127 mm. and the larger end from 140 to 152 mm. in diameter. The largest individual ball that was collected and measured in the case of Jap weighed 1.85 kg., had a length of 216 mm., and diameters at the two ends of 127 and 152 mm., respectively. A popular impression that prevails among elephant men is that the first ball in the passage of feces is the largest, the next one is smaller, and the last smallest of all. For this reason a few measurements were made of each successive bolus discharged in several of the defecations. The information obtained on Jap with regard to this particular point was by no means conclusive, as it was deemed of secondary importance to the study of other factors. Strictly speaking, these measurements, to be precise, should be made on balls of feces before they strike the ground and become misshaped or possibly broken. To supplement the observations with Jap by more accurate measurements, when the feces of the Barnes herd were studied the successive boluses were collected in three large, wire-mesh scoops.[1] Even under these conditions the collection of boluses without damage was by no means perfect, since the attempt was also made to collect simultaneously both urine and feces for the study of their temperatures. In a few instances, however, the collections of the individual boluses were reasonably well carried out, and the results of the measurements are given in table 26. There appears to be no regularity in the order in which the various sizes of bolus appear. In one instance the heaviest ball appeared first and in two instances the lightest appeared first. There was little difference in the diameters of the balls in any given defecation, except that in two instances the first bolus was longer than the second and third. It is also a question as to whether there is any correlation between the size of the animal and the size and weight of the bolus. The boluses of the two small animals in the Barnes herd, Nos. 58 and 61, weighed approximately 600 grams, had lengths of 105 and 79 mm., respectively, and diameters[2] at the small end of 121 and 114 mm. and at the large end of 133 and 133 mm., respectively. These weights and measurements are, in general, smaller than those noted with the boluses of the larger elephants.

TABLE 26—*Measurements of individual boluses of elephant feces*

Elephant No.	Bolus	Weight	Diameters	Length
		kg.	*mm.*	*mm.*
48	First	1.29	133, 121, 133, 114	146
	Second	1.12	152, 111	111
	Fourth	1.12	140, 146, 127	124
52	First	1.0	124, 124	178
	Second	1.63	162, 168, 127	146
	Third	1.41	165, 146, 127	130
53	Third	1.175		
55	Third or fourth	1.15		
58	Third or fourth	.610	133, 121	105
61	Third or fourth	.590	133, 114	79
62	First	1.19	156, 127	140
	Third	1.3	152, 152, 133	143

Stimulus to defecation—It is the experience of elephant men that the animals defecate frequently and in large masses at the time of any unusual excitement. Thus, prior to their going on the cars at night they ordinarily defecate copiously. From the æsthetic standpoint, showmen do not wish elephants to defecate or urinate while performing in the ring. Hence all performing elephants are subjected to a "cleaning out process" prior to ring performance. This can be done in two ways. In India the mahout is said to remove the balls of feces by inserting the hand and arm in the rectum.[1] The common method in American circuses, however, is to subject the elephants by a word of command to physical exercise before they enter the ring. This exercise consists of standing up on the hind legs at intervals of ten or fifteen seconds for a number of times during a period of about fifteen minutes. After such exercise most elephants defecate and urinate. Thus the rectum is temporarily cleared, and no feces are passed during the performance. The absence of a well-adjusted keeper prevented this procedure in the study of Jap's feces. If defecations could have been secured upon command, the study could have been much more carefully made. Jap could neither be stimulated to defecate nor be made to stand up. It can be easily seen, however, that the separation of feces in a digestion study could be made probably better with an elephant thus trained than with any other animal. Even humans can not defecate on command, and certainly other animals do not. It would be ideal in digestion studies if the feces could be passed at given hours comparable to the times for the beginning and end of 24-hour collections of urine. The elephant always has a large mass of feces either in the rectum or continually approaching it, ready to be discharged on stimulus. What is the stimulus to defecation in the case of the normal elephant, which defecates not far from twenty times per 24 hours? With Jap, for example, examination of the weights per defecation, as recorded in table 24, shows that the stimulus to defecate obtains when the amount to be discharged would be not far from 5 or 6 kg., this being the weight of the average discharge. On the other hand, in a number of instances defecation did not take place until from 10 to 11 kg. of feces had accumulated. A notable example is offered by the data on April 7. At 12.38 a.m. seven balls of feces were passed, weighing 6.67 kg. One hour later nine balls were passed, weighing 10.43 kg. The maximum weight of a single defecation was 10.97 kg. on April 6 at 6.30 p.m. During the nine days there were, however, six instances when the fecal discharge amounted to over 10 kg. Jap usually defecated after standing up. Defecation was possibly induced by the physical exertion of standing up or, conversely, Jap may have been stimulated to stand up as a result of the accumulation of feces in the intestinal tract and the urge to defecate. No certainty exists regarding this point, however, for not infrequently Jap passed feces while lying down. With the Ringling herd in Florida it was also observed that feces were not infrequently passed when lying down. A similar experience is reported by various zoological garden keepers. It was further noticed with the Ringling herd that the desire to defecate or urinate seemed to be invariably the stimulus to rise after lying down, for the animals almost invariably urinated and defecated immediately upon standing up. Indeed, advantage was taken of this stimulus to collect feces from individual elephants at different times.

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[1] In these collections and in the simultaneous collection of urine samples we were given every aid through the enthusiastic cooperation of the assistant trainer, Mr. John Noble.

[2] Measured at two or more points.

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[1] Evans, G. H., *Elephants and their diseases,* Rangoon, 1901 and 1910.

Chemical Composition of Feces

Since there are no recorded analyses of the composition of elephant feces, this type of study was incorporated in our research. The observations included an analysis of an individual sample of Jap's feces obtained on March 12, 1935, an analysis of a composite sample of Jap's feces collected during the 9-day digestion experiment from April 2 to April 11, analyses of individual samples from the two elephants at Franklin Park (Nos. 2 and 3), and analyses of individual samples from seven of the elephants in the Barnes herd (Nos. 48, 52, 53, 55, 58, 61, and 62), the working herd that performed a large amount of severe muscular work and were fed a somewhat larger amount of grain than the average circus elephant. These analyses (made in duplicate on each sample) were kindly carried out for us under the direction of Professor E. G. Ritzman of the University of New Hampshire. The results, calculated on the basis of water-free substance, are given in table 27.

The water content of Jap's feces, 77 per cent, was higher than that of the feces of the other elephants. With elephants Nos. 2 and 3 the water content averaged 74 per cent, definitely higher than that noted with the Barnes herd. With one of the elephants in the Barnes herd (No. 62) the water content was as low as 65 per cent and with another (No. 48) 60 per cent. This difference in water content was not apparent to the eye. All of the elephant feces examined seemed relatively dry, in fact, much drier than cow feces and seemingly as dry as, if not drier than, the ordinary feces of the horse.

For comparison with these analyses of elephant feces there have been included in table 27 the previously published results of analyses of the feces of a number of steers. In all instances these steers, like Jap, received a hay ration only and were fed at a maintenance level except in the last four instances, when a submaintenance ration of about half the maintenance amount of hay was fed. Likewise we are fortunate in having in hand a recent report of an unpublished analysis (given to us by Professor E. G. Ritzman) made on the feces of a horse fed exclusively on a maintenance ration of timothy hay. With the steers and the horse on maintenance hay rations, the water content of the fresh feces is much more nearly 80 per cent. The comparison of these several analyses for water content bears out fully the impression gained from visual inspection. Thus, freshly passed elephant feces are strikingly different in appearance from the feces of the steer and the horse (in general more nearly approximating the appearance of horse feces), and the percentage of water in elephant feces is relatively low. Indeed, there is nearly 4 per cent less water in fresh elephant feces such as those passed by Jap and Nos. 2 and 3 than there is in the fresh feces of the average steer on maintenance hay rations. Even when steers are on submaintenance hay rations, when their feces are much harder and more pilular in form, the water content is not so low as that found with the elephant. Furthermore, elephant feces contain less water than even the seemingly hard and less moist horse feces. Judged from ocular impression, therefore, relatively small changes in the water content of feces make striking differences in their apparent consistency.

TABLE 27—*Chemical composition and energy value of water-free substance in feces*

Date or observer	Animal	Elephant No.	Ash	Ether extract	Crude fiber	Nitrogen	Protein (N x 6.25)	Nitrogen-free extract	Energy per gram of		Water content of fresh feces
									Water-free substance	Water-free and ash-free substance	
1935			*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*cal.*	*cal.*	*p. ct.*
Mar. 12		Jap	7.40	3.16	41.52	0.83	5.17	42.75	4.658	5.031	76.7
Apr. 2–11[1]		Jap	5.60	3.32	40.28	1.04	6.51	44.29	4.821	5.107	76.3
Sept. 4		2	8.66	6.34	34.96	1.31	8.18	41.52	4.884	5.347	74.6
Sept. 4		3	5.45	6.38	34.26	1.30	8.11	45.80	5.127	5.422	73.4
Aug. 1		48	10.49	3.48	36.57	.87	5.44	44.02	4.578	5.115	59.9
Aug. 1		52	10.65	3.79	36.58	.87	5.43	43.55	4.551	5.094	68.0
Aug. 1		53	9.73	4.17	36.74	.89	5.54	43.82	4.610	5.107	69.6
Aug. 1		55	7.61	3.97	37.96	.95	5.93	44.53	4.797	5.192	70.9
Aug. 1		58	7.27	4.94	37.30	1.07	6.69	43.80	4.852	5.233	69.7
Aug. 1		61	9.67	3.40	38.01	.90	5.60	43.32	4.663	5.162	74.8
Aug. 1		62	7.52	4.23	39.07	.92	5.76	43.42	4.745	5.130	64.9
Benedict and Ritzman[2]	Steer A		8.90	3.82	29.52	1.56	9.74	48.02	4.780	5.247	82.6
	Steer B		8.74	3.96	29.88	1.59	9.91	47.51	4.740	5.194	81.3
Zuntz[3]	Steer		11.20	6.07	23.15	1.83	11.42	48.16	4.693	5.285	82.1
Armsby[4]	Steer A		5.67	2.12	39.94	1.38	8.61	43.66	4.861	5.153	79.6
"	" "		5.63	2.11	41.08	1.30	8.10	43.08	4.791	5.077	82.8
"	Steer B		5.87	2.18	38.52	1.58	9.88	43.55	4.894	5.199	78.1
"	" "		6.50	2.05	39.55	1.53	9.58	42.32	4.833	5.169	79.8
Benedict and Ritzman[5]	Steer A		9.60	3.71	26.09	1.63	10.19	50.41	4.724	5.226	80.9
	" "		8.52	3.52	26.43	1.50	9.36	52.17	4.804	5.252	78.6
	Steer B		9.24	3.74	26.69	1.63	10.21	50.12	4.839	5.332	80.6
	" "		8.62	3.67	27.24	1.50	9.35	51.12	4.751	5.199	79.7
Ritzman[6]	Horse		8.00	3.21	34.42	1.27	7.94	46.43	4.678	5.085	82.7

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[1] Jap's feces of April 2-11 contained 1.48 mg. of sodium chloride per gram of water-free substance.

[2] Benedict, F. G., and E. G. Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, tables 27 and 28, pp. 127 and 129. Steers fed maintenance rations of hay only.

[3] Von der Heide, R., Klein, W., and N. Zuntz, Landw. Jahrb., 1913, **44**, pp. 769 and 812. Steer fed hay only.

[4] Armsby, H. P., and J. A. Fries, U. S. Dept. Agric., Bureau Animal Industry, Bull. 128, 1911, p. 233; experiments in 1905. Steers fed hay only.

[5] Benedict, F. G., and E. G. Ritzman, *loc. cit.* Steers fed submaintenance hay rations.

[6] Unpublished analyses furnished by Professor E. G. Ritzman of the University of New Hampshire. Horse fed exclusively a maintenance ration of timothy hay.

The marked resemblance between dried feces and what would be the appearance of chopped hay as fed to the elephant leads to a comparison of the composition of the feces of Jap and the hay fed to Jap during the digestion experiment on April 2 to 11. The composition of the hay on the water-free basis has already been reported on page 165. The comparison shows that the composition of the water-free feces was essentially the same as that of the water-free hay, the only noticeable difference being that the water-free feces contained about 1.5 per cent more of ash, 1.5 per cent more of fat, and 4 per cent more of crude fiber.

Since our study of the respiratory exchange of the elephant was made with only one animal, it was realized that careful observations with this same elephant regarding other physiological factors would contribute information as to whether this particular elephant was essentially normal or not. Hence it is of special interest to compare the chemical constituents of Jap's feces with those of the feces of the other elephants. The two samples analyzed for Jap, one a chance sample obtained in March and the other a composite sample for the digestion experiment in April, show in general substantial agreement in the various chemical constituents, and the differences are probably no greater than one would expect in two samples of feces on the same day. With the other elephants the lowest percentage of ash (5.45 per cent with No. 3) is a little lower than the lower of the two percentages noted with Jap. On the other hand, with at least two of the Barnes herd (Nos. 48 and 52) the percentages of ash are much higher than even the higher of the two percentages found with Jap. In making these comparisons one should recall that the Barnes herd, being the working herd, was fed a much more liberal ration than Jap and also salt, which Jap did not have. The percentage of ether extract was larger in the case of all the other elephants than it was with Jap, and especially high with Nos. 2 and 3. These two latter instances possibly reflect the percentages of oil meal in the diet. No reliable comparison of the characters of the diets of these different elephants can be made, however. The crude fiber content was notably higher in Jap's feces than in those of the others, undoubtedly attributable to the fact that she was fed exclusively hay and a rather poor quality of hay. The nitrogen content[1] of Jap's feces was not unlike the percentages observed in the case of the more liberally fed Barnes herd, but appreciably lower than the percentages found with Nos. 2 and 3. What is true of the nitrogen content is also true of the protein content. The content of nitrogen-free extract, commonly called total carbohydrate, was essentially the same with all the elephants, not far from 43 to 44 per cent. The energy per gram of water-free substance and per gram of water-free and ash-free substance in the case of Jap was much the same as noted with the other elephants. The slightly higher energy values of Nos. 2 and 3 are reflected in the percentages of ether extract. From this comparison it is clear that the few marked differences noted in the composition of the several samples of feces can be explained by the differences in the types of feed received by the elephants. There is, therefore, every reason to believe that from the standpoint of chemical composition Jap's feces were characteristic of elephant feces in general.

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[1] The experience of workers with domestic animals has led to extreme precautions to avoid or to correct for losses of nitrogen in the drying process. It is worthy of record here that, surprisingly enough, no significant loss of nitrogen by drying was noted with the elephant feces.

Because of the variability noted in some of the chemical constituents of elephant feces in some instances, it does not seem justifiable to draw average values for the composition of elephant feces from all the data recorded in table 27 for this animal. Perhaps the most reasonable procedure would be to average those values for the elephants other than Jap. This, however, has not been done. Hence a comparison of the elephants' feces with those of the steers can be made only from general inspection of the data in the table rather than by the use of any specific average values.

With the steers listed in table 27 there was no significant difference in the composition of water-free feces, whether the animal was fed a full ration or a submaintenance ration of hay. The content of nitrogen-free extract was a little higher and the crude-fiber content a little lower when submaintenance rations were fed to the steers, indicating perhaps that the crude fiber was somewhat more thoroughly attacked by bacterial fermentation, but the percentages of the other ingredients remained essentially unchanged at both feed levels. With Armsby's steers the percentages of ash, ether extract, and nitrogen-free extract were notably lower and the crude-fiber content was higher than with the other steers, but the nitrogen and protein contents were essentially the same as with the others. These differences are undoubtedly explained by the fact that the hay fed to Armsby's steers was lower in ash, ether extract, and nitrogen-free extract and higher in crude-fiber content than was the hay fed to Benedict and Ritzman's steers.

On the whole, the elephants' feces contained somewhat higher percentages of ash and ether extract than did those of the steers, and the percentages of crude fiber were much higher than those noted with the steers, except for Armsby's steers, and slightly higher than the percentage found in the one sample of horse feces. In the case of Armsby's steers the crude-fiber content of the feces was the same as that in the elephants' feces. This is to be expected, because the crude-fiber content of the hay fed to these steers was actually somewhat higher than that fed to Jap. The nitrogen content was lower in the elephants' feces than in those of the steers. The percentages of nitrogen-free extract were lower with the elephants than those found with the steers studied by Benedict and Ritzman but much the same as those found with Armsby's steers. The most marked differences, however, occur in the crude-fiber percentages. Macroscopic examination of elephant feces shows that they are characterized by the presence of a large amount of seemingly unaltered hay. This would imply that a large proportion of the crude fiber in the hay had been unfermented. This is borne out, in general, by the high percentages of crude fiber noted in the several samples of elephant feces.

Comparison of the composition of the feces of the horse (subsisting on a maintenance ration of timothy hay only) with the composition of elephant feces shows that the amount of ash in horse feces is materially higher than that in Jap's feces for April 2 to 11 (when a more complete analysis was made), but is about the same as the average ash content in the feces of the Barnes herd of elephants. The percentage of ether extract is essentially that noted with the elephants, except for Nos. 2 and 3. The crude-fiber content of the horse feces is measurably lower than that of Jap's feces and somewhat lower than the percentages found in the Barnes herd analyses, but the same as that for elephants Nos. 2 and 3. The high percentage of crude fiber in Jap's feces suggests again that a very poor quality of hay was fed to this animal. The nitrogen and likewise the protein content is of no special significance. The percentage of nitrogen-free extract in the horse feces is 46.43, slightly above that in the elephant feces but a little below that in the feces of the under-nourished steers. The heat of combustion of the horse feces likewise is essentially that noted with all the other animals.

The most striking single factor noted in the examination of the feces of the elephant is the extraordinarily poor subdivision of the food materials eaten by these animals, for, as stated on page 177, the feces are substantially unaltered hay.[1] This speaks for a very poor mastication. It is surprising that apparently so little use of the grinding surfaces of the teeth is made by the elephant. This suggests that a real service, both to palæontology and physiology, could be done by at least a macroscopic study of freshly dropped elephant dung in the forests of Africa and in the wild in India, the object being to note the nature of the feces when the animals are subsisting upon their normal feed, in no wise controlled by man. But analyses in the field are out of the question; however, samples could easily be preserved for subsequent analysis, and it is hoped that such observations will be ultimately forthcoming. As the matter stands now, certainly with the feed as controlled by man, the grinding surface of the elephant's tooth seemingly plays a wholly insignificant rôle in its life.

RATE OF FOOD PASSAGE THROUGH INTESTINES

A matter of considerable concern is the length of time that food remains in the intestinal tract of the elephant. Obviously because of the presence of bacteria and because the body temperature favors fermentation, the longer the food remains in the intestines the greater the possibility for bacterial action. The study of the mechanics of defecation of the elephant suggests that the food stays inside the body for a rather short period. Furthermore, the relatively small (though from the size of the animal absolutely large) amounts of fermentation gases continually escaping through the rectum and in the air expired from the trunk of the elephant (see page 244) and the fact that the odor from these gases is not excessively disagreeable suggest that, although there is some fermentative action, the food can not remain very long in the intestines. Information regarding this problem is desirable from the standpoint of studying the digestibility of food in the case of the elephant. In the digestion experiment with

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[1] Unaltered oats are frequently noted in elephant feces, but their appearance is of slight quantitative significance. Even succulent feed may be passed unaltered in the feces, as demonstrated by the finding of portions of red beets, unattacked, in the feces. (See page 171.)

Jap an attempt was made to feed her for a sufficient length of time and to collect the feces over a sufficient period to have the feces represent qualitatively and quantitatively the average fecal mass from the ration fed. In this type of experiment the time period should be such that a definite weight of feces can be legitimately ascribed to a definite weight of food intake. With humans and other animals, certain devices are employed to mark the feces. Thus, with humans and dogs a coloring material, such as cochineal or lamp black, or a material that results in a certain consistency in the feces (for example, undigestible seeds) is fed with the first meal of the true digestion experiment. The feces are then carefully collected, all that part of the fecal mass containing the first sign of the coloring matter or the seeds and everything following this are retained (any feces ahead of the coloring matter are rejected), and the feces passed thereafter are considered to belong to the experimental period. At the end of the experiment the coloring matter is given again with the first meal following the digestion experiment, and any feces colored by this material are excluded from that belonging to the fecal mass collected during the digestion period. This type of feces separation is difficult with animals that discharge large masses of feces, especially if the feces are loosely formed, as is the case with ruminants. In such instances the clever method of Edin[1] of Stockholm (who employs chromic oxide and makes chemical determinations of the amount of chromic oxide in the feces) is most successful.

In the case of Jap the only method practicable for carrying out a digestion experiment was to extend the period of observation over as many days as possible, on the assumption that the fecal masses discharged would be representative of the food intake during the same period of time. This procedure is far from satisfactory, but there was no alternative. Although the chromic oxide method and the use of coloring material were not employed, a study to obtain information on this point was made by the following procedure. Jap was fed a number of pieces of rubber of different shapes and sizes, cut from an inner tube of an automobile tire. Ten pieces of rubber, from 28 to 97 mm. long and from 8 to 37 mm. wide, were placed inside a loaf of bread and given to Jap. Every bolus of feces passed thereafter was opened with a fork and carefully examined, to note when the first piece of rubber appeared. The time for the appearance of each successive piece of rubber until the last was found was also carefully recorded. This particular type of experiment was carried out on four occasions with Jap, and the results are reported in table 28.

On April 2 at 12.45 p.m. ten pieces of rubber were fed. The first two pieces were recovered in the defecation at 12.40 p.m., April 3, or almost exactly 24 hours later. The last piece was found 41 hours after the rubber was given, the length of time between the appearance of the first and the last piece being approximately 17 hours. On April 3 at 6.36 p.m. ten pieces of rubber were again given, as a matter of fact, before the last piece of the first experiment had passed through the animal. The second ten pieces were especially marked, however, so that there would be no confusion. The first pieces of the second lot appeared in 21 hours. The last piece was not obtained for 54 hours and 34 minutes. The rubber was so badly disintegrated, however, that there was no way of being certain that all had been recovered. In this case the difference between the appearance of the first piece of rubber and the appearance of the last piece was 33 hours. The rubber was usually found near the center of the ball of feces.

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[1] Edin, H., Nordiske Jordbrugsforskeres Forenings, Kongress i København, July, 1921, p. 388.

Table 28—*Elapsed time before pieces of rubber fed to elephant Jap appeared in feces*

Date and time rubber was fed	Number of pieces fed	Elapsed time before recovery of First piece		Elapsed time before recovery of Last piece	
1935		*hr.*	*min.*	*hr.*	*min.*
Apr. 2, 12.45 p.m.	10	23	55	41	15
Apr. 3, 6.36 p.m.	10	21	0	54	34
Apr. 5, 11.46 a.m.	10[1]	29	38	46	14
Apr. 8, 10.30 a.m.	5	30	25	51	45

[1] Only four pieces found in feces.

The significant fact is that in all four tests the first piece of rubber appeared after from 21 to 30 hours. Rarely were all the pieces recovered intact. A number of them were broken up. In general, however, the results of these tests indicate that food residues of any given feeding begin to pass out of the body from the intestinal tract of the elephant in about 24 hours and completely disappear from the body in about 50 hours.

The loaf of bread in which the pieces of rubber were placed was, as is common, wrapped in paraffin paper. Jap ate the entire loaf, including the paper. The chemical resistance of paraffin paper would lead one to think that this should ultimately appear in the feces. A most careful search was made in the feces for scraps of this paper, but it was never identified as such. It is reasonable to suppose that the paper was of such fragile nature that it could not withstand the continual churning with the large amount of roughage (hay) and that it was disintegrated merely by passage through the alimentary tract, without any considerable amount of preliminary tearing by the teeth. Indeed, the impression was that the loaf of bread was too rapidly swallowed (see page 168) for the elephant to have taken any time for comminution.

The appearance of the rubber pieces recovered from the feces varied greatly. The first set given came through practically intact. In most of the other sets about half of the pieces were intact and the other half considerably broken up, seemingly by teeth action. The general impression of the man who fed the bread to Jap was that it was swallowed instantly or very slightly chewed. On the other hand, it would seem hardly possible that even the crude, fibrous, rough hay particles in the intestinal tract could of themselves, in connection with the powerful muscular movements of the intestinal tract, churn up and actually destroy and disintegrate pieces of live rubber 10 cm. long and 2 to 4 cm. wide, the rubber being from 2 to 3 mm. thick. Such breaking up of rubber speaks strongly for at least a partial use of teeth.

The stimulus to the rapid passage of food through the intestinal tract may be varied. With steers fed upon roughages the time for food residues to appear in the feces is usually from a day and a half to two days. If soft, succulent material is fed, this time may be shortened to from 12 to 30 hours. The actual appearance of food residues in the feces, however, may in part depend upon the nature of the food and character and length of the intestinal tract. Relative to its great size, the length of the intestinal tract of the elephant is short. Autopsies seem to indicate a length of not far from 100 feet (30 meters), yet the length of the elephant's intestinal tract is essentially the same as that of such domestic animals as the horse, the mule, and, indeed, the sheep and the goat. This would indicate that the food remains for a somewhat shorter time in the intestinal tract of the elephant. The tremendous volume of very poorly digested hay consumed by the elephant (if one accepts the theory of roughage influencing peristaltic action) would also tend to hasten the passage of food through the intestinal tract. All of these considerations are in direct confirmation of the fact that tests with rubber pieces in the food of the elephant showed a rapid passage through the intestinal canal.

The general conclusion is that food passes through the intestinal tract of the elephant fairly rapidly. This is in large part due to the fact that the elephant is not a ruminant, and hence has no large feed reserve or ballast comparable to that of ruminants. It has already been pointed out (see page 107) that the intestinal contents of the elephant may represent from 7 to 12 per cent of the total body weight, and that with a ruminant like the steer this inert mass may be as much as 40 per cent of the total weight. This rather rapid passage of food through the intestinal tract of the elephant should have two pronounced effects on the digestibility of the food. In the first place, the time for the reaction of the digestive juices is relatively short, and this of itself would make for a lowered digestibility. Secondly, the time for bacterial fermentation is much shorter than with other animals, and although the bacterial fermentation may not be looked upon as an economic energy transformation, nevertheless the greater the bacterial action, the greater the apparent digestibility of the food or the greater the amount of food elements disappearing from the hay.

APPARENT DIGESTIBILITY OF HAY BY THE ELEPHANT JAP

The expression "apparent digestibility" is used in its broadest sense to indicate the percentage of any one of the chemical constituents or energy in the hay that does not appear in the feces. It does not take into consideration whether this material has been used for body processes or has been dissipated in the form of products of fermentation. Innumerable digestion experiments with ruminants and other Herbivora indicate that their digestive processes differ profoundly from those of Omnivora and birds in that large amounts of methane and carbon dioxide are formed as a result of bacterial action in the paunch. It is a serious question whether this bacterial transformation is of any economic advantage to the body from the standpoint of energetics. The paunch is a great incubating oven at about 36° C. The ferments are, therefore, continually at work under ideal conditions, attacking particularly the carbohydrates and the cellulose. The materials that are destroyed by ferments and bacteria do disappear from the intestinal tract, but not as a result of body tissue activity. Hence in all probability they have no economic use in the body. Nevertheless, as such material is not found in the feces, it is by common usage considered as digested or, better, "apparently digested."

Because of the fairly rapid passage of food through the intestinal tract of the elephant, the relatively small production of methane (see page 253), the poor mastication of food, and the large amounts of almost unattacked hay noticed in the feces of Jap and other elephants, one would infer that the digestibility of hay by this animal would in all probability be low. Consequently in any attempt to compute the energy intake of the elephant from the weights of hay consumed, one could not assume that the standard digestibility factors noted with goats, sheep, horses, or cows would necessarily apply to the elephant. For this reason a digestion experiment was carried out with Jap, to secure information not only from the purely physiological standpoint but likewise from the standpoint of the economics of feeding these great animals. Experimenters with large domestic animals recognize that the ordinary marker or, indeed, the Edin method, is not so generally applicable for the separation of the feces during a digestion trial as is the more practical method of feeding the animal at a certain level for a number of days or weeks and then arbitrarily selecting a certain length of time during these days or weeks when all the feces are collected and weighed and all the feed is weighed. This latter procedure was carried out in the digestion experiment with Jap. It is greatly regretted that the short time at our disposal and the uncertainty of the animal's remaining at Campgaw for any prolonged period because of its professional engagements, which obviously had to be given first consideration, made it necessary to limit the study of digestibility to a shorter feeding period than would otherwise have been preferred. The general requirement of a 3-week feeding period could not be met. Furthermore, the feeding prior to the test period could not be regulated, for during this time Jap was moved into New York and out to Campgaw again and again. There is every reason to believe that before the digestion experiment she was fed hay only, but there may have been variations in the quality and the amounts fed. On the whole, however, it is believed that she never was fed to excess.

A 9-day digestion period was the longest that could be carried out. This began at midnight on April 2 and ended at midnight on April 11. During this time all the feed given to Jap was weighed, any feed not eaten was also weighed, all the feces passed were collected and weighed, and aliquot samples of both feed and feces were collected and subsequently subjected to chemical analysis. The quantitative measurement of the feed intake and more particularly the complete collection of the feces meant constant vigilance and a responsible attendant with the animal the entire time. To carry out this painstaking experiment, therefore, two thoroughly trained assistants, George Lee and Carl Hatch of the Nutrition Laboratory, were sent to Campgaw, New Jersey, and made complete unbroken collections and weighings of samples day and night, in relays, during the nine days.

Collection, weighing, and sampling of feces—At the start of the digestion experiment a canvas was placed under Jap's hind legs to prevent contamination of the feces with earth or bedding. Later, when the canvas became badly soiled and torn, a large sheet of galvanized iron was placed under her and this proved more satisfactory. The moment feces were dropped they were collected from the canvas or sheet metal, placed in a suitable container, and weighed. Each defecation was then broken and stirred thoroughly with a spading fork in a washtub. Then 2 per cent of the mixture was placed in a glass preserve jar containing 10 cc. of a 10-per cent solution of thymol in chloroform. Several of these jars were filled in a day. At the end of the digestion period, the contents of all the jars were dried to an air-dry condition, and then were thoroughly mixed. From this mixture a representative sample was taken for analysis. The fact that Jap's feces were passed in such hard masses made it impossible to follow out the carefully developed method of aliquoting of feces so generally used at the University of New Hampshire by Professor Ritzman, who has the feces of steers and cows shovelled, quartered, and sub-divided much as cement. The work involved in collecting the feces and the hay for nine days was such that more careful separations and aliquoting could not be carried out. But the analyses of the feces of other elephants (see table 27, page 186) show that the composition of the feces of elephants on maintenance hay rations does not vary greatly. Any error of aliquoting, therefore, is probably well within the limit of the inherent errors introduced by the shortness of the period of investigation, the considerable irregularity in the amount of feed eaten per day, and the possible variations in the quality and the quantity of the hay fed prior to the actual beginning of the digestion experiment.

Measurement of feed intake—For a complete digestion experiment it is obviously as important to know the amount and the composition of the food eaten as it is to have information about the feces. The feed eaten by Jap during the digestion period was almost exclusively hay. The few instances when insignificant amounts of other foods were given to her (see table 22, page 164) can be neglected. The use of only one food material simplified the measurement of the food intake. Since, however, there was no adequate storage of hay in the barn where Jap was quartered and since the enormous amounts of hay required for each day's feeding could not be weighed, properly sub-divided, and aliquoted before each day began (as would be done in ordinary tests with ruminants), the methods of weighing and aliquoting of the hay were rather crude. The procedure in weighing the hay has already been explained on page 163.

The Nutrition Laboratory dislikes to present an experiment of this kind as a careful study of digestibility, but the exigencies under which the measurements had to be made and the enormous masses of both hay and feces that had to be handled left no time for developing a more precise method.

Since hay alone was fed, there can not have been a great error in obtaining a representative sample of the feed.

The results of the chemical analyses of the aliquot samples of hay and feces and the recorded weights of hay intake and fecal outgo have already been discussed on pages 163, 165, 181, and 185. The weights of the chemical constituents in the hay and the feces and the apparent digestibility of each of these several constituents (that is, the difference between the weight of the ingredient in the feces and the weight of the ingredient in the hay referred to the total weight of that ingredient in the hay) are recorded in table 29. It has already been pointed out (see page 187) that the chemical composition of Jap's feces was essentially the same as that of the hay she ate, except that the feces had slightly higher contents of ash, fat, and crude fiber. Theoretically, therefore, one could almost determine the apparent digestibility by referring the dry matter in the feces to the dry matter in the hay. On this basis the hay was 44 per cent digestible. In our cooperative researches with Professor E. G. Ritzman at the University of New Hampshire[1] and in the investigations of Professor Armsby[2] the digestibility of dry matter in timothy hay has been found to be in general from 50 to 55 per cent with steers on maintenance rations and a few per cent higher with steers on submaintenance rations of this hay (approximately one-half the maintenance rations). With cows on maintenance rations of timothy hay, unpublished experiments at the University of New Hampshire show an apparent digestibility of dry matter of hay, ranging from 49 to 68 per cent and averaging about 60 per cent. With the horse fed on various kinds of hay, Armsby[3] reports an apparent digestibility of dry matter ranging from 47 to 58 per cent, and with sheep from 56 to 65 per cent. With two horses on maintenance rations of hay, oats, and straw Zuntz and Lehmann[4] found

TABLE 29—*Apparent digestibility of constituents in hay eaten by the elephant Jap*

	Hay	Feces	Apparent digestibility
	kg.	*kg.*	*p. ct.*
Total weight in 9 days	449.08	979.92	....
Dry matter	413.00	232.24	43.8
Ash	17.47	13.01	25.5
Nitrogen	4.68	2.42	48.3
Protein	29.24	15.12	48.3
Ether extract	7.81	7.71	1.3
Crude fiber	150.25	93.55	37.7
Energy (calories)	1,858,500.	1,114,752.	40.0
Nitrogen-free extract	208.23	102.86	50.6

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[1] Benedict, F. G., and E. G. Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, pp. 131 *et seq.*

[2] Armsby, H. P., and J. A. Fries, U. S. Dept. Agric., Bureau Anim. Industry, Bull. 128, 1911, pp. 27 *et seq.*

[3] Armsby, H. P., *The nutrition of farm animals,* New York, 1917, p. 605.

[4] Zuntz, N., and C. Lehmann, Landw. Jahrb., 1889, **18**, pp. 147 and 152.

that the digestibility of dry matter amounted to 52 and 60 per cent, respectively.

The apparent digestibility is of greatest significance from the standpoint of energy. With Jap the apparent digestibility of the energy content of the feed was 40 per cent. With steers on maintenance rations of timothy hay it has been found to be about 50 per cent.[1] With cows on maintenance rations of timothy hay, unpublished experiments carried out at Durham, New Hampshire, show a digestibility of energy varying from 47 to 67 per cent and averaging more nearly 60 per cent. These calculations of the apparent digestibility of the energy content do not take into consideration the effect of fermentation upon the utilization of the food energy. If one interprets heat given off by an animal as a waste product, as indicated by Armsby, the heat of fermentation certainly comes under this head. However, an animal has an essential need for heat for its own tissues that must be met by the energy of the food. There is no demand that methane be produced for the vital processes of the body. Hence the methane represents a complete economic loss. It is assumed that the energy in the hay that does not appear in the feces has been utilized by the body. Further discussion of this point will be left until the treatment of the energy balance, following the report of the respiration experiments. (See page 271.)

Comparison of the percentages of digestibility of dry matter and energy noted with the elephant and with other animals demonstrates what was surmised from the general appearance of the feces, namely, that the elephant makes an extraordinarily poor utilization of the ingredients of the hay. The apparent digestibility of the dry matter of feed, for example, appears to be lowest with the elephant, next lowest with the horse, higher with the steer, the cow, and the sheep, and highest with the rabbit. To what extent these differences are associated with differences in the animals' habits of mastication and to what extent fermentation plays a rôle can at best be only a matter of speculation. More than likely both factors play a rôle. From the practical standpoint the question is whether any method can be employed to improve the digestibility of hay eaten by elephants. One instantly thinks of the possibility of chopping the hay, to aid in its mastication and better utilization. Although Armsby[2] points out that the digestibility of coarse fodders is not increased by cutting, since the organic matter is digested to about the same extent whether it is cut or finely ground, nevertheless it is a fair question as to whether, with the elephant, cutting the hay, not necessarily grinding it, might not result in greater utilization. This cutting might take the place of better comminution both in the initial chewing and in the digestion phase. When elephants are in winter quarters, chopping of the hay would not be impracticable, but when they are on tour it would be. It might be better to feed silage, but here again, although not impossible to do this in winter quarters, it would be impossible on tour. Too little is known with regard to the digestibility of concentrates by elephants. If one were to judge from experience with other animals, one would expect with the elephant a much higher digestibility of concentrates than of hay, perhaps a much higher digestibility proportionately than is noted with other animals. If this should prove to be true, the question naturally arises as to whether feeding of concentrates to elephants, even at a higher cost per ton than the cost of hay, would not be a sounder practise than the exclusive use of roughages.

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[1] Benedict, F. G., and E. G. Ritzman, Carnegie Inst. Wash. Pub. No. 324, 1923, p. 136.

[2] Armsby, H. P., *The nutrition of farm animals*, New York, 1917, p. 624.

This digestion study on Jap, although by no means complete, suggests that much remains to be done to determine, both from the economic and the physiological standpoints, the best rations to be given to the elephant, an animal that represents a very large financial investment and for which the cost of maintenance is large. Recognition must be given to the necessary difference between the rations during the stay in permanent winter quarters and the rations during the exhibition tours, which frequently cover tens of thousands of miles in a season and which are characterized by numerous administrative and transportation problems.

URINE

When one considers the large amounts of money invested in elephants in various parts of the world, their great economic value, and the importance of maintaining them in good health, one is astonished that so few measurements have been made on this animal similar to those made in clinics on humans to assess their health. Thus, so far as we are aware, there are no reported analyses of feces, either chemical or microscopic, and only partial analyses of urine. Apparently the first attempts to make a scientific study of the urine of the elephant were the observations by Vogel[1] and by Vauquelin and Fourcroy,[2] but the methods and observations reported by them are such that they can not be interpreted in the light of present-day methods of analyzing urine. There have also been brief statements regarding characteristics of the elephant's urine by Colin[3] and by Evans,[4] but other than these records apparently no analyses, either qualitatively or quantitatively, have been made.[5] Since contact with other animals has shown that in suspected cases of internal metabolic disturbance the kidneys have been found to function abnormally, knowledge of the physiology of the urine of the elephant is prerequisite for future studies on the pathology of this animal. In this survey of the physiology of the elephant, therefore, it was believed important to make a number of urine analyses on supposedly healthy animals. For this reason urine samples were collected from the elephant Jap on four days in March, and during the nine-day digestion experiment in April consecutive collections of her urine, approximating as nearly as possible 24-hour collections, were made by the same two observers who had charge of the feces collection. In addition, single specimens of urine were collected from twenty-nine of the thirty-four elephants in the Ringling herd, all nine elephants in the Downie herd, fifteen of the elephants in the Barnes herd, and the two elephants at the Boston Zoological Park. Thus the urine survey was representative of fifty-six elephants, all but one of which were females and all of which were Asiatic. That so many of the findings from these urine analyses are contradictory to the commonly accepted characteristics of elephant's urine (as will be pointed out in subsequent pages) is doubtless to be explained by the fact that our analyses were made on urines from a large number of elephants, whereas the earlier results probably represent only fragmentary observations on one or two specimens. We are far from satisfied, however, with our survey of the elephant's urine and believe that 24-hour collections with, if possible, quantitative measurements of the food intake are needed. The desirability of such a study is emphasized, when one considers the great economic value of the elephant. A thorough understanding of the physiology of this animal will make it possible to study their pathology better and from such a study to derive therapeutic measures.

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[1] v. Vogel, H. A., Journ. f. Chemie u. Physik, 1817, **19**, p. 156.

[2] Fourcroy, A. F., and L. N. Vauquelin, Journ. Soc. d. Pharm., Paris, **1**, p. 129. (Cited by D. J. C. Reil, Arch. f. d. Physiol., Halle, 1800, **4**, p. 162.)

[3] Colin, G., *Traité de physiologie comparée des animaux,* Paris, 1888, 3d ed., **2**, pp. 848, 849, and 854.

[4] Evans, G. H., *Elephants and their diseases,* Rangoon, 1901 and 1910.

[5] As this report is about to go to press, our attention has been called to the analyses of elephant urine by M. Takamatsu (Journ. Biochem., Tokyo, 1935, **21**, pp. 427 and 435), too late, however, to make extensive comments on them in our text.

Collection and Sampling of Urine

The collection of urine from the elephant presented an unusual problem, for the elephant never urinates while lying, but does urinate almost simultaneously with the passing of feces. The genitalia of the female elephant are well forward, occupying much the position of the udder in the case of the cow, and the urine is delivered slightly forward of the rear legs. Hence collection of urine from the rear was practically ruled out, and the collection had to be made from the side. Usually the external genitalia are lowered appreciably just prior to urination, and thus there is some previous indication of when the animal is about to urinate. The female assumes a characteristic position when about to urinate, spreading the legs with the obvious intent of not having the urine wet them. Elephants employed for exhibition purposes are frequently made to urinate before the performance by reaching under the body and patting the genitalia or breasts with the hand or, more commonly, by making them exercise (*i.e.*, stand up) to provoke defecation as well as urination. (See page 184.)

At the outset it was difficult to know what size containers were necessary to hold the complete urination, for the estimates of the volume of a urination made by different elephant men varied from two or three quarts to several gallons. In the urine study on Jap an attempt was made at first to place a wide-mouthed 10-gallon milk can under her from the side, but Jap kicked it over. A 5-gallon garbage can with wider opening but of lower height was likewise kicked over occasionally but for the most part tolerated. An attempt was also made to catch the urine in a long, gum rubber fishing boot, attached to a pole, but this also Jap resented and no success attended its use. Throughout the entire period of observation, Jap frequently prevented the collection of urine by kicking over the container or destroying whatever implement was used for the collection. This happened particularly between midnight and morning, when she seemed especially to resist attempts at collection. Whether this was due to the presence of the observers who were active in the barn and kept her awake or whether the light in the barn necessary to read the scales kept her awake and made her irritable is not certain. Hours were spent in trying to obtain complete 24-hour specimens, only to have the attempt defeated by a sudden movement on the part of the animal. The only loss of urine, however, was when the animal upset it; at no time was it lost by being voided before the assistant could place a container under the elephant. This disinclination of Jap to have the urine collected was an idiosyncrasy of an animal having otherwise a pleasant disposition. Undoubtedly if Jap had had a keeper at that time who understood her cues, this resentment of urine collections could have been overcome and she could have been made to urinate on command. Under such conditions undoubtedly more complete 24-hour collections of urine could have been made. As it was, the collections during the digestion trial were as complete as possible, and the times when urinations occurred were recorded, the total amount of each urination collected was weighed, and two or three samples were preserved for later analysis. Even when the larger part of the volume of a urination had been spilled from the container by the animal, a sample of whatever portion was caught was taken for analysis. Hence, although the urine collections could not be separated into exact 24-hour periods, nevertheless the data obtained do contribute information regarding the chemistry of the urine. In the case of the other elephants, where one specimen only (and that not quantitative) was collected, the urine was caught in a wide-mouthed thermos-jar held in the stream of urine. (See page 141.)

In every instance duplicate samples were made of each collection of urine. The urines of the Ringling elephants were preserved with 2 cc. of a solution of 10 per cent thymol in chloroform. Those of the Downie and the Barnes herd were preserved with xylene.

After the urine voided by Jap had been weighed, a 100 cc. sample was preserved with chloroform containing 10 per cent thymol by weight, to make possible a determination of the chlorides and at the same time to prevent decomposition. A duplicate 100 cc. sample was preserved with chloroform, thymol, and hydrochloric acid to hold the ammonia and to make possible the determination of creatine and creatinine. These samples were subsequently subjected to chemical analysis at the Nutrition Laboratory, as explained on page 26. A third sample of Jap's urine was sent to the New England Deaconess Hospital in Boston, Massachusetts, for microscopic examination (see page 201). Samples of urines from the Ringling herd were sent for microscopic examination to the Eastern Maine General Hospital in Bangor, Maine, and samples from the Barnes herd to the hospital in Calais, Maine. Since it is considered highly advantageous to make this examination as soon as possible after the urine is voided, so that there will be the least disintegration of the destructible elements in the urine, any samples for microscopic examination were delivered at the hospitals either by messenger or (in the case of the Boston hospital) by air mail. In these instances no preservative was used except for Jap's urines, which were placed in bottles containing a suitable preservative supplied by the hospital. In addition to this type of examination, all samples were analyzed for total nitrogen content and nearly all were subjected to qualitative tests for sugar and albumin. The chemical constituents of the urines and the heats of combustion were determined in many instances. Thus, aside from the fact that there were no complete 24-hour collections of urine, a reasonably detailed survey of the physical and chemical characteristics of the urine samples obtained was made, from which certain deductions can be drawn regarding this feature of the elephant's physiology.

Frequency of Urination

Day versus night—In the wild the elephant is in large part a nocturnal animal. In captivity it remains for the major portion of the day and night awake and on its feet and is almost continually feeding, but water is not accessible to it at all times. In the zoological park and in the circus the elephant is usually given water twice a day, morning and night, so that from this standpoint the day may be considered to be separated into two 12-hour periods, the night extending from 6 p.m. to 6 a.m. and the day from 6 a.m. to 6 p.m. The frequency of urination during the day and the night may be expected naturally to reflect the habits of the elephant. With Jap during the digestion study in April, records were kept of the times of urination during each successive twenty-four hours. (See tables 16 and 30, pages 143 and 206.) From these records the frequency of urination during the day and the night, with the division of the twenty-four hours at 6 a.m. and 6 p.m., has been determined, with the following results:

April	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10–11	Avg.
Night	7	5	6	6	4	4	5	6	4	5
Day	5	6	5	4	4	4	4	3	4	4

Usually Jap urinated somewhat more frequently at night than during the day. In one 24-hour period the situation was reversed, and in three 24-hour periods there was an equal number of urinations both day and night. Since frequency of urination would be determined solely by stimulus and since most animals urinate infrequently at night because asleep, the more frequent urination at night by the elephant is to be explained by its general living habits, particularly its nocturnal habits. Jap objected to attempts to collect her urine, and it was often noted that she tried to retain the urine. This may account for the fact that on the successive days of the digestion study, the total number of urinations per 24 hours gradually decreased and that on the last day, April 10-11, the total number of urinations was but two-thirds that on the first day.

Relation to drinking water—Jap was given water twenty-four times during the digestion experiment. In twenty-one instances urination followed fairly soon after the drinking of water. Of these instances ten occurred from 6 to 32 minutes after drinking, three at the time of drinking, and the remaining eight from 1 to 3½ hours after drinking. Although Jap was usually given water twice a day, morning and night, there was some unavoidable irregularity in drinking. However, the data do give information regarding the relationship between the time of urination and the drinking of water and show that in general the drinking of water was quickly followed by urination.

PHYSICAL PROPERTIES

Color, odor, and clarity—The urines of the various elephants studied were straw or amber in color and had no pronounced odor. This latter feature is in harmony with the fact that elephant feces have much less odor than is the case with other animals. The urines were in many instances clear but more frequently turbid, at times extremely so, even when freshly voided. This was noted also on innumerable occasions when urine samples were not collected for analysis. With the Ringling herd, independent observations as to the degree of clearness were made both at the time of collection of the samples and after the samples had reached the laboratory where they were examined. In most cases the two observations agreed. In five instances the urines were turbid rather than clear at the time of collection and subsequently, when examined in the laboratory, they had become clear. It may be concluded that elephant urine, as voided, is in general turbid.[1]

Reaction—In those specimens in which a test of the acidity or alkalinity was made, the reaction was acid in fourteen instances, neutral in eight, and alkaline in fifteen.

MICROSCOPY

So little is known with regard to the microscopy of elephant urine that opportunity was taken whenever possible to have microscopic tests made at the earliest possible moment after the urine was voided, to obviate any disintegration by standing. In the case of Jap the samples were collected late in the afternoon and shipped by special delivery from Campgaw so that they reached the laboratory table in Boston at 8 o'clock the next morning. Thus Jap's samples were almost invariably examined under the microscope within fourteen hours after the urine had been passed. Dr. H. F. Root and Miss H. W. Hunt in Dr. Joslin's laboratory at the New England Deaconess Hospital in Boston kindly arranged to expedite these tests on Jap's urines so that the reports of the microscopy can be stated to have been made upon fresh material. Special attention was given to the microscopic examination of Jap's urine owing to the legend that she was suffering from "kidney trouble." Nobody knew what the symptoms were, but this legend had apparently existed for years. In the seven specimens of urine collected at about 6 p.m. on different days between April 2 and April 10 microscopy showed either no albumin or only the slightest possible traces. Examination of one sample for blood, casts, and pus showed that none of these was present. In five of the samples there was no sugar, in one a trace of sugar, and in one 0.1 per cent, respectively. All the specimens, however, were loaded with calcium oxalate crystals. Dr. Root states that the true sediment of Jap's urine was so thick that it could hardly be examined. The larger, coarser particles of the sediment were, therefore, allowed to settle. The cloudy fluid remaining was then put under the microscope, and it was this fluid that showed the large number of calcium oxalate crystals. There was no bile and no diacetic acid in any of the samples. Microscopy, therefore, gives no support to the legend that Jap had "kidney trouble."

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[1] Colin, G. (*Traité de physiologie comparée des animaux,* Paris, 1888, 3d ed., 2, p. 854), states that the female elephant discharges a clear urine. Evans states that the urine is clear, but toward the end of the voiding may be a little turbid.

The microscopic study of the urines of thirty-one of the elephants in the Ringling herd, made in the laboratory of Dr. H. E. Thompson in Bangor within a few hours after the samples were collected, confirms the findings of Dr. Root on Jap's urine, namely, that the urine contains enormous amounts of calcium oxalate crystals. In addition, in nine instances a few leukocytes were found, in two instances a few ammonium urate crystals, and in nine instances a few epithelial cells, but albumin and sugar were absent in all samples. Short strings of mucus were noted in one sample.

With the Downie herd, whose urines were also examined in Dr. Joslin's laboratory, specimens were obtained from four of the animals within a half-hour following a street parade about six miles in length, from two animals before the parade, and from three other animals in the exhibition tent later in the day. The traces of albumin in the urines of these elephants were very slight. Sugar was absent in five cases and present only in mere traces in four cases. No casts or pus were found in any of the samples, and blood was present in only one sample. In two specimens the appearance of bacteria was noted, but this might well have been due to outside contamination. In only three samples was an examination made to determine the presence of calcium oxalate crystals. In two of these a few crystals were present, and in one there were many. There was no suggestion of anything abnormal in the urines of the Downie herd, and the results in general were the same as those obtained on Jap and the Ringling herd.

The urines of the Barnes herd, collected at St. Stephen, New Brunswick, were hurried across the river to the hospital of Dr. W. N. Miner in Calais, and there examined microscopically by Dr. Kenneth Russell, who reports that albumin was not present except in one instance, when there was a very slight trace. Sugar was absent in all cases. There were no blood cells, but the sample that showed the slightest possible trace of albumin contained a few tubular casts.

The general conclusion is that the elephant's urine is characterized by a large preponderance of calcium oxalate crystals, and that the abnormal constituents found in pathological human urine are rarely found in the urine of the elephant.

Volume of Discharge

The ideal prerequisite in the study of human urine, namely, a complete 24-hour collection, at first seemed feasible to carry out with Jap but subsequently proved to be impracticable under the working conditions that obtained, in spite of constant vigilance night and day on the part of two assistants during the 9-day digestion study with Jap. It is obvious that analyses of 24-hour collections of elephant urine are imperatively needed and present no great problem other than patience and the time involved. During the period when these animals are in winter quarters such experiments, especially on well-trained individuals, should not be impossible. Although collection of the total 24-hour volume of urine could not be accomplished, reasonably complete collections of the individual urinations of Jap were made, and these were accurately weighed. Furthermore, when losses unavoidably occurred due to Jap's movements, rough estimates were made of the probable amounts lost. The weights of the individual collections of urine have already been reported in table 16. The volumes of the individual collections (calculated from the weights of urine and the specific gravities) are given in table 30, page 206, as well as the estimated volumes lost, the specific gravities, and the nitrogen content per cubic centimeter of urine. No attempt has been made to correct the volumes as collected for the estimated amounts lost.

As in so many instances the complete volume of urine voided was not collected, an average value for the volume of an individual urination may be questioned. Nevertheless an average has been drawn for all the collections between 5.40 p.m. on April 2 and 10.02 p.m. on April 11, which indicates that the average individual discharge is 5.5 liters (1½ gallons). The variability in the volumes of the individual urinations is striking. In five instances the volumes collected amounted to 9 liters or more, and the maximum individual discharge was 10.58 liters (2¾ gallons). Hence the bladder capacity was almost double the volume of the average discharge. The size of the seemingly tremendous discharge of urine by the elephant is invariably over-estimated, the maximum volume being stated by several attendants to be nearer 10 gallons than 10 liters (2½ gallons).

Nothing can be said with regard to the variability in the volumes of individual urinations with reference to the time of day, for there were too many instances when the complete volume of a urination was not collected.

TOTAL VOLUME OF URINE EXCRETED PER 24 HOURS

From the admittedly unsatisfactory data regarding the volumes of the individual urinations, the total 24-hour volume of urine discharged by Jap can be calculated in several ways. The volumes of all individual urinations during the observations in April can be added, this result increased by the estimated volumes lost, and the total volume thus obtained divided by the total time represented, and converted to the 24-hour basis. By this method the average volume per 24 hours is 52.4 liters. Since Jap weighed 3672 kg., the 24-hour volume per kilogram of body weight would be 14.3 cc. Since one of the urinations on April 3 was completely lost except for the small amount obtained as a sample for analysis, and many other collections did not represent the complete volumes discharged, this method of calculation gives results that are too low.

A second method is to add the volumes of individual urinations in those instances only when the collections were complete, divide by the total number of minutes represented by these complete collections, and multiply by 1440. According to this calculation 173,701 cc. of urine were collected without loss in 78 hours and 15 minutes, or on the average 53.3 liters per day (14.5 cc. per kilogram). The most logical method, however, is to calculate to the 24-hour basis each one of the volumes representing a complete collection of an individual urination, based upon the time represented by that particular collection, and to average the 24-hour values thus computed. Properly speaking, the 24-hour values thus obtained should be weighted in proportion to the lengths of time covered by the periods of collection. Without such weighting, the average total 24-hour excretion by this method of calculation becomes 59.7 liters and that per kilogram of body weight becomes 16.3 cc.

It is clear that the longer the period of collection, the more highly probable it is that the volume of urine collected closely approximates the true 24-hour volume. If only the longest periods of complete collection are used for this type of calculation, one should consider, for example, the period of 16 hours and 28 minutes, from 1.18 p.m. on April 5 to 5.46 a.m. on April 6, when the complete volume collected was 32.2 liters. Per 24 hours this would be 46.9 liters. The next longest period of complete collection lasted 12 hours and 53 minutes (from 9.15 a.m. to 10.08 p.m. on April 10) during which the total volume amounted to 24.3 liters or, expressed per 24 hours, 45.2 liters. On the basis of these two longest periods the total 24-hour volume would be nearer 46 liters than the estimate of 60 liters obtained by the averaging of all the 24-hour estimates based upon all the complete collections. In all probability the true value lies somewhere between these, and a round figure can be accepted of approximately 50 liters per 24 hours as the total volume of urinary discharge by an elephant weighing 3672 kg., or 13.6 cc. per kilogram of body weight per 24 hours. These two values based upon the experiments with Jap can, in the absence of complete 24-hour collections, be accepted as reasonably probable.

Results of Chemical Analyses

Dr. Thorne M. Carpenter of the Nutrition Laboratory kindly took the responsibility of having the urine analyses made, discussed with the writer the significance of the results obtained, and prepared for inclusion in this report particularly the sections dealing with the interpretation of the results on the partition of the nitrogenous constituents of the urine. We are extremely grateful to him for the time and effort he has put upon this study.

SPECIFIC GRAVITY

In view of the apparently authoritative statement of Evans[1] that the specific gravity of elephant urine is 1.004, that is, unusually low, the first record obtained on a sample of Jap's urine showing a specific gravity of 1.028 challenged attention immediately. The question arises as to whether the volume of urine discharged was extraordinarily small for the removal of waste products or whether there were some factors in the urine other than nitrogenous. The high specific gravity first noted in Jap's urine was likewise challenging because this large animal was on a protein-poor and not particularly liberal ration, and the digestibility of the ration was not high. It was thought that an explanation for the high value might be that the drinking water contained an excessive amount of salts. Jap drank large volumes of water, and if the water contained a large amount of soluble salts, this would tend to raise the specific gravity. As has already been pointed out, however, she could obtain from this source only about 17 grams of solids per day. (See page 176.) As other samples of Jap's urine were studied, it was noted (see table 30) that the specific gravities were not uniformly so high as at first reported, but on no occasion was as low a value found with Jap as that of 1.004 reported by Evans. In the first study with Jap, the lowest value was 1.015 and the average was 1.025. In the second study the first specimen sent to Boston had a specific gravity of 1.032. With the several samples studied on subsequent days there were a number of instances of low gravities. Thus, on April 2 at 9.05 p.m. a value of 1.006 was noted, on April 4 at 7.25 p.m. 1.008, on April 10 at 10.08 p.m. 1.007, and about forty minutes later 1.005. Although these low gravities were not invariably associated with very large volumes, the two volumes of urine on April 10 of 6554 and 5781 cc., added together, represent a large discharge. In these two instances, consequently, the low gravities were apparently associated with a large volume of urine in the bladder. On the whole, however, no definite relationship between volume of discharge and specific gravity can be established. The largest individual discharges, that is, those of 10 liters or over (but three such discharges occurred), had specific gravities of 1.021, 1.020, and 1.013. Although the variability in the values is wide and no attempt has been made to weight any of them in association with the volume, the averaging of the results indicates that the average specific gravity of Jap's urine was 1.023. This is confirmed by the average of 1.022 noted in the analyses of the composite samples of urine made up daily during the April series. (See table 32.)

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[1] Evans, G. H., *Elephants and their diseases,* Rangoon, 1901 and 1910.

The striking difference between this average value, based upon ninety-five determinations, and the 1.004 reported by Evans and the fact that in a few instances Jap's urines showed gravities as low as 1.010 (with an absolute minimum of 1.005) led to the conviction that other analyses were imperative before any conclusion could be drawn as to the specific gravity of elephant's urine. The physiological significance of an average value representing the specific gravity of elephant's urine may be no greater than that of the average value ascribed to human urines, which today plays little rôle, owing to the more intimate knowledge of the chemical composition of human urine and the influence of diet. Nevertheless the specific gravities were determined in the urines of many of the elephants in the three herds studied, and the results, together with the records of nitrogen per cubic centimeter of urine, are recorded in table 31.

In a number of instances, specific gravities were determined in different hospitals as well as at the Nutrition Laboratory. The rather considerable differences in the temperatures at which the observations were made were almost without significance in the final results. But since the picnometer and the urinometer methods may involve slight corrections (which ordinarily need not be applied to the values obtained in regular clinical work), the specific gravities in the urine samples from the elephant herds were also determined at the Nutrition Laboratory by the use of the Westphal balance, an instrument of precision. All the results reported in table 31 were obtained at the Nutrition Laboratory by this latter method, so that on this basis they are all comparable and the averages derived therefrom for the several herds of elephants may be considered to give a fair picture of the specific gravities.

Of the twenty-eight values recorded for the Ringling herd, the lowest is 1.009, the highest 1.033, and the average 1.019. With the Downie herd, which included one male elephant, the minimum is 1.016, the maximum 1.031,

Table 30—*Volume, specific gravity, and nitrogen in the urine of the elephant Jap*

Date and time	Volume		Specific gravity	Nitrogen per cc. of urine
	Collected	Lost (estimated)		
1935	*cc.*	*cc.*		*mg.*
Mar. 11				
9.38 a.m.	973	......	1.028	4.16
10.58 a.m.	2515	......	1.022	4.03
6.00 p.m.	7287	......	1.032	6.48
Mar. 12				
9.10 a.m.	1642	......	1.029	4.71
10.45 a.m.	6749	......	1.015	1.59
12.28 p.m.	2734	......	1.017	3.09
Mar. 17				
2.28 p.m.	6329	......	1.027	5.00
Mar. 18				
10.25 a.m.	2502	......	1.027	4.01
Apr. 2				
1.15 p.m.	......	......	......	......
5.40 p.m.	4971	470	1.032	6.01
7.41 p.m.	2911	300	1.027	3.87
8.49 p.m.	5623	(2)	1.012	.86
9.05 p.m.	6014	(1)	1.006	.66
11.15 p.m.	8873	......	1.020	1.32
Apr. 3				
2.55 a.m.	......	(3)	1.024	3.51
4.18 a.m.	1846	(2)	1.024	2.91
5.58 a.m.	3359	(2)	1.024	2.86
8.11 a.m.	4269	(2)	1.026	3.41
10.25 a.m.	4721	......	1.021	3.18
12.40 p.m.	5902	250	1.020	2.91
1935	*cc.*	*cc.*		*mg.*
Apr. 6				
12.09 a.m.	5166	......	1.026	5.05
2.25 a.m.	5200	(1)	1.027	4.61
5.46 a.m.	6641	......	1.027	5.24
8.05 a.m.	5073	200	1.033	5.11
11.36 a.m.	4530	......	1.033	7.14
2.18 p.m.	5998	20	1.032	5.33
5.24 p.m.	4277	(2)	1.031	5.84
8.19 p.m,	5223	......	1.030	5.78
11.52 p.m.	5581	......	1.032	6.48
Apr. 7				
3.50 a.m.	5767	(2)	1.030	5.93
5.35 a.m.	3226	(2)	1.029	5.67
8.58 a.m.	6839	......	1.028	5.68
11.42 a.m.	5287	(2)	1.027	5.64
1.35 p.m.	7256	(2)	1.013	2.39
5.20 p.m.	8594	(1)	1.024	4.80
9.03 p.m.	7585	(2)	1.027	5.25
10.46 p.m.	5327	......	1.025	3.54
Apr. 8				
12.30 a.m.	5171	......	1.021	3.90
3.50 a.m.	7500	200	1.024	4.56
6.54 a.m.	5499	1000	1.022	4.10
8.46 a.m.	3473	......	1.025	5.33
12.10 p.m.	7073	470	1.025	5.12
3.40 p.m.	7483	20	1.025	4.84

2.10 p.m.	4417	(2)	1.021	2.52
4.15 p.m.	4547	1000	1.016	2.68
6.05 p.m.	5616	1500	1.015	2.20
7.38 p.m.	3094	(2)	1.018	2.76
9.54 p.m.	5201	(2)	1.019	3.15
11.06 p.m.	2971	(2)	1.020	2.51
Apr. 4				
2.21 a.m.	9393	....	1.021	2.73
6.00 a.m.	10264	200	1.021	2.75
8.49 a.m.	9011	(2)	1.021	2.84
9.46 a.m.	2951	(2)	1.020	2.67
11.10 a.m.	4114	(2)	1.021	2.91
2.14 p.m.	8483	(2)	1.022	2.91
5.39 p.m.	7476	(2)	1.022	3.27
6.46 p.m.	5751	....	1.012	1.70
7.25 p.m.	3512	(2)	1.008	.80
7.59 p.m.	8495	500	1.010	.85
10.50 p.m.	7888	....	1.018	3.08
Apr. 5				
12.17 a.m.	4275	(2)	1.020	2.54
2.26 a.m.	5996	(2)	1.019	2.99
6.05 a.m.	9951	(2)	1.020	3.56
8.53 a.m.	6634	(1)	1.022	3.59
11.30 a.m.	4417	4000	1.021	3.27
1.18 p.m.	3763	300	1.023	3.73
3.41 p.m.	3978	....	1.023	4.59
6.40 p.m.	4188	....	1.022	5.34
7.59 p.m.	3395	....	1.022	4.65
9.53 p.m.	3597	....	1.023	5.41
6.50 p.m.	3275	1000	1.029	6.51
9.14 p.m.	4732	....	1.025	5.41
11.45 p.m.	3633	(2)	1.024	5.92
Apr. 9				
1.33 a.m.	3268	(2)	1.025	4.87
2.50 a.m.	3070	(1)	1.026	5.28
6.27 a.m.	8094	....	1.029	5.42
9.26 a.m.	4971	....	1.026	5.88
11.36 a.m.	3200	(2)	1.028	6.97
4.55 p.m.	5496	(2)	1.028	8.12
6.32 p.m.	4697	....	1.024	5.28
8.54 p.m.	10582	....	1.013	2.81
11.02 p.m.	3307	(2)	1.028	6.62
Apr. 10				
12.19 a.m.	3304	....	1.026	5.03
1.59 a.m.	3509	(2)	1.026	4.85
4.45 a.m.	5326	....	1.029	5.64
9.15 a.m.	6547	(2)	1.028	6.16
1.20 p.m.	5874	....	1.030	7.13
4.35 p.m.	6456	....	1.027	5.38
8.38 p.m.	5385	....	1.027	6.65
10.08 p.m.	6554	....	1.007	1.75
10.45 p.m.	5781	1000	1.005	1.27
Apr. 11				
2.25 a.m.	8768	(2)	1.015	3.53
6.10 a.m.	6974	(2)	1.021	4.64
7.44 a.m.	2791	....	1.021	4.82
1.00 p.m.	6018	50	1.027	6.86
5.00 p.m.	3496	(2)	1.027	7.10
10.02 p.m.	6898	(2)	1.025	5.66

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[1] A few drops of urine were lost.

[2] Some urine lost; amount not known.

[3] Total lost, except sample.

and the average 1.023. With the Barnes herd the picture is different, for with two animals minimum values of 1.004 (precisely that reported by Evans) were noted. The maximum value, 1.025, was found with two elephants. In view of this picture it is a matter of regret that more precise knowledge is not at hand regarding the total daily discharge of urine and the total daily intake of food by the animals in the Barnes herd. These elephants differed strikingly from the other herds of elephants in that they were heavily fed and did a great deal of work. *A priori,* one would have expected that their urines would have been more concentrated than those of the other elephants. Certainly they performed a great deal more work than the others, and although there was no visible perspiration, the metabolism must have been greatly increased during the work, with a larger output of water vapor, entirely aside from the urinary output. Because of this effect of the work and the undoubtedly higher protein intake, the assumption might have been made that the urine would be more concentrated and have a higher specific gravity. It was a matter of considerable astonishment,

Table 31—*Specific gravity and nitrogen in urine—elephant herds*

Elephant No.	Specific gravity	Nitrogen per cc. of urine	Elephant No.	Specific gravity	Nitrogen per cc. of urine
Ringling herd		*mg.*	Downie herd		*mg.*
14	1.012	2.27	5	1.031	6.53
15	1.015	3.14	6	1.016	3.24
16	1.033	6.39	7	1.026	4.50
17	1.010	1.74	8	1.025	4.22
18	1.015	2.90	9	1.023	4.79
19	1.022	6.12	10	1.022	5.31
20	1.026	5.10	11	1.027	6.80
21	1.020	4.86	12	1.017	4.88
22	1.029	7.86	13	1.017	5.76
23	1.009	1.64			
24	1.018	4.30	Average......	1.023	
25	1.022	5.26			
26	1.010	2.31			
27	....	3.68	Barnes herd		
28	1.027	4.88	48	1.025	6.17
29	1.018	3.75	49	1.022	6.75
30	1.021	4.66	49	1.022	6.88
31	1.022	4.54	50	1.025	7.11
32	1.017	3.48	51	1.019	5.96
34	1.022	4.17	52	1.024	7.67
35	1.027	4.63	53	1.004	1.47
36	1.025	4.26	53	1.009	3.47
37	1.018	3.40	54	....	5.93
38	1.025	4.40	55	1.004	1.62
39	1.016	3.01	55	1.011	4.18
40	1.015	2.25	56	1.015	4.68
41	1.010	2.25	57	1.010	3.67
42	1.025	4.92	58	1.016	4.99
44	1.011	2.40	59	1.016	5.42
Average......	1.019		Average......	1.016	

therefore, to find that the lowest gravities in the entire study occurred with two of the elephants in this working herd, and that the average specific gravity noted with this herd, 1.016, is lower than the averages obtained with the other two herds. This emphasizes again the importance of making a more precise physiological study from this standpoint, not only of the normal, non-working elephant but particularly of the working and highly fed elephant.

To report an average figure to be taken as representing the specific gravity of the urines of elephants as a whole is unscientific, because it is well known that with humans the specific gravity of the urine under normal conditions varies from hour to hour. Indeed, the variability of the specific gravity is a well-known test of the functioning of the kidneys with humans. Since, however, the general picture of the specific gravities of a large number of specimens of elephant urine, as recorded in tables 30 and 31, is so widely divergent from the one specific gravity recorded in the literature, an average value has been derived as follows. The average specific gravities in the case of the three herds were 1.019, 1.023, and 1.016, respectively. The average value for Jap is 1.023. Since this represents only a single animal, it can not be averaged directly with the three averages for the herds. But it is clear that an average for the elephant in general could be justifiably given as essentially that noted with the Ringling herd, namely, 1.019. Obviously wide variations can be expected from this average value, not only with the same elephant at different times of the day but with different individuals, as is shown by the details given in tables 30 and 31. Thus the range with Jap alone was from 1.005 to 1.033 and with the fifty-one elephants in the herds, upon which this type of observation was made, from 1.004 to 1.033.

TOTAL SOLIDS

Although the discussion of the quantitative aspects of elephant urine is defective, inasmuch as complete 24-hour collections were out of the question, nevertheless it seems justifiable to consider the various quantitative factors with special emphasis upon any ratios that may be established between the individual constituents of the urine. As a source of the excretion of unoxidized material, the urine can not be neglected in any consideration of the energy balance. Hence the total solids and particularly the organic solids in the urine should be known. The total solids, ash, and organic matter were determined in the composite samples of Jap's urines, which represent reasonable approximations of 24-hour collections, and in the individual specimens obtained from the Barnes herd. (See tables 32 and 33.) Because of the uncertainty regarding the total volume of urine discharged per day, the results of the analyses of the various constituents in the urine are reported only per cubic centimeter of urine. The method of making these determinations was to pipette out 10 cc. in a small, porcelain, evaporating dish and to dry at 90° C. until the dish plus contents had reached a constant weight. This gave the total solids in the urine. The dish and contents were then placed over a gas flame and burned at low red heat until the weight of the dish plus ash was constant. The material remaining in the dish after ignition was considered to be ash.

TABLE 32—*Solids in the urine of the elephant Jap*

Period of collection of composite sample[1]		Specific gravity	Total solids		Ash		Organic matter per cc. of urine	Nitrogen per cc. of urine	Organic matter divided by nitrogen
Date[1]	Time		Per cc. of urine	Referred to specific gravity[2]	Per cc. of urine	Per cent of total solids			
1935			*mg.*		*mg.*		*mg.*	*mg.*	
Apr. 2– 3	1.15 p.m.– 2.10 p.m.	1.019	35.0	1.84	6.71	19.2	28.3	2.94	9.6
Apr. 3– 4	2.10 p.m.– 2.14 p.m.	1.019	32.1	1.69	6.70	20.9	25.4	2.66	9.5
Apr. 4– 5	2.14 p.m.– 1.18 p.m.	1.016	26.0	1.63	6.93	26.7	19.0	2.47	7.7
Apr. 5– 6	1.18 p.m.–11.36 a.m.	1.024	45.1	1.88	8.39	18.6	36.7	5.11	7.2
Apr. 6– 7	11.36 a.m.– 1.35 p.m.	1.026	56.7	2.18	9.60	16.9	47.1	5.47	8.6
Apr. 7– 8	1.35 p.m.–12.10 p.m.	1.024	45.4	1.89	8.55	18.8	36.8	4.58	8.0
Apr. 8– 9	12.10 p.m.–11.36 a.m.	1.025	48.4	1.94	10.95	22.6	37.5	5.58	6.7
Apr. 9–10	11.36 a.m.– 1.20 p.m.	1.026	51.7	1.99	9.34	18.1	42.4	5.86	7.2
Apr. 10–11	1.20 p.m.– 5.00 p.m.	1.018	37.3	2.07	6.43	17.2	30.9	4.48	6.9
Apr. 11	5.00 p.m.–10.02 p.m.	1.025	54.3	2.17	6.11	11.3	48.1	5.60	8.9

[1] The data for 5.00 p.m. to 10.02 p.m. on April 11 represent the analyses on one individual sample of one voiding. The data for the other dates represent analyses of composite samples of several voidings during the time indicated. All samples were preserved with chloroform and thymol.

[2] Grams of total solids per liter of urine divided by the value represented by the figures in the second and third decimal places of the specific gravity.

With Jap the total solids ranged from 26.0 to 56.7 mg. per cubic centimeter and with the Barnes herd from 6.75 to 51.38 mg. per cc. A close relationship between the total solids and the specific gravity is to be expected. Thus, the lowest specific gravity noted with Jap, 1.016, is accompanied by the lowest total solids, 26.0 mg., and similarly the highest gravities (1.026 in two instances) are accompanied by high total solids, in one instance absolutely the highest amount of total solids (56.7 mg.) and in the other a high value of 51.7 mg. This same relationship is noted with the Barnes herd.

TABLE 33—*Solids in urine—Barnes herd*

Elephant No.	Specific gravity	Total solids		Ash		Organic matter per cc. of urine	Nitrogen per cc. of urine	Organic matter divided by nitrogen
		Per cc. of urine	Referred to specific gravity[1]	Per cc. of urine	Per cent of total solids			
		mg.		*mg.*		*mg.*	*mg.*	
48	1.025	50.63	2.03	13.93	27.5	36.70	6.17	5.9
49	1.022	37.18	1.69	8.08	21.8	29.10	6.75	4.3
49	1.022	38.45	1.75	9.15	23.3	29.30	6.88	4.3
50	1.025	46.10	1.84	11.68	25.4	34.42	7.11	4.8
51	1.019	35.30	1.86	7.20	20.4	28.10	5.96	4.7
52	1.024	51.38	2.14	8.63	16.8	42.75	7.67	5.6
53	1.004	6.75	1.69	1.70	25.3	5.05	1.47	3.4
53	1.009	15.18	1.69	2.98	19.6	12.20	3.47	3.5
54	....	33.18	....	7.73	23.3	25.45	5.93	4.3
55	1.004	8.03	2.01	1.55	19.4	6.48	1.62	4.0
55	1.011	20.65	1.88	4.18	20.2	16.47	4.18	3.9
56	1.015	27.98	1.87	6.18	22.1	21.80	4.68	4.7
57	1.010	18.23	1.82	3.78	20.8	14.45	3.67	3.9
58	1.016	34.43	2.15	6.13	17.9	28.30	4.99	5.7
59	1.016	29.20	1.83	6.25	21.3	22.95	5.42	4.2
Average	1.016	30.18	1.88	6.61	21.7	23.57	5.06	4.5

[1] Grams of total solids per liter of urine divided by the value represented by the figures in the second and third decimal places of the specific gravity.

RATIO OF TOTAL SOLIDS TO SPECIFIC GRAVITY

In clinical studies on humans it was the custom for many years to compute the total solids in urine from the specific gravity by means of the Roberts factor 2.33. Thus it has been found that with ordinary conditions of diet the total solids in one liter of urine may be approximated by multiplying the last two figures of the specific gravity (as ordinarily expressed in three decimal places) by 2.33. Since in the case of Jap both the specific gravity and the total solids were determined, the calculation can be reversed to determine the factor that should be applied to the specific gravity. Thus, in the fifth column of table 32 the first factor of 1.84 has been obtained by dividing the total solids per liter of urine (35 grams) by the last two figures of the specific gravity (19). With Jap the values for this factor thus calculated all lie very much below 2.33 and average 1.93. With the Barnes herd the factors average 1.88. Since the character of the food determines in large part the specific gravity of the urine in that it influences markedly the material voided in the urine, and since there was a wide difference in the character of the rations fed to Jap and the Barnes herd, it is surprising that the factors are so close in these two instances. Jap was fed exclusively on hay and the Barnes herd received, in addition to hay, a considerable amount of oats and bran and an allotment of salt. Salt in the urine raises the specific gravity much more than does urea, for example.

Although there is considerable variability in the factors as calculated for the Barnes herd (the range being from 1.69 to 2.15), nevertheless the average value of 1.88 may be taken as representing with reasonable closeness the relationship between the specific gravity and the total solids. One could, therefore, logically compute the total solids discharged in a day's time in the urine of an elephant, if one knew the total 24-hour volume of urine discharged and the specific gravity of the urine.

Of special interest in this study of the total solids is the fact that from the calculations on Jap it can be seen that the elephant may readily lose in the urine per day from 2 to 3 kg. of solids, of which a considerable portion may be organic material with potential energy and hence a factor in the energy balance.

Constituents of Total Solids

Ash

Correlation between ash and specific gravity—Complete mineral analyses and separation of the various solid constituents of the urine were not made, but the ash was determined in the urines both of Jap and the Barnes herd. (See tables 32 and 33.) With Jap there appears to be no direct correlation between the ash per cubic centimeter of urine and the specific gravity. To be sure, the highest ash content in the case of Jap's urine (10.95 mg.) is associated with a specific gravity of 1.025. On the other hand, the lowest ash content (6.11 mg.) is associated with the same specific gravity. This suggests that there could not have been a large proportion of mineral solids in Jap's urine. With the Barnes herd a correlation between the ash content and the specific gravity is clearly shown, for the lowest specific gravities of 1.004 are associated with less than 2 mg. of ash per cubic centimeter of urine, and the highest specific gravities with over 10 mg. of ash.

Correlation between ash and total solids—The determinations of the percentage of ash in the total solids of Jap's urines show a wide variability (from 11.3 to 26.7 per cent) and an average of 19 per cent. The percentages of ash in the total solids of the urines from the Barnes herd range from 16.8 to 27.5 per cent and average 22 per cent, perceptibly higher than was the case with Jap. These values for the ash content and the percentages of ash in total solids indicate that there was a larger proportion of mineral matter in the urines of the Barnes herd than in the urines of Jap, thus confirming what one would normally expect from the rather imperfect information regarding the feeding of this herd and the feeding of Jap. It has previously been stated that the factor of 1.88 might reasonably be applied to the determination of the specific gravity to calculate the total solids in the urine of an elephant. In a 31-day fast by a man at the Nutrition Laboratory the ratio of total solids to specific gravity was, on the last 16 days of the fast, 3.2.[1] Since the excretion of chlorine by this fasting man was extremely low, such figures would with man more closely approximate that of the elephant on hay alone (not being allowed any salt), and we have here an indication of a definitely higher specific gravity with man than with the elephant. On the other hand, the percentage of ash in the total solids is, on the average, 19 and 22 per cent with Jap and the Barnes herd, respectively, and with men on 2- to 7-day fasts the ash averaged 21 per cent of the total solids in urine.[2] This comparison shows that in general, both with fasting men and with the well-fed elephant, the mineral matter in the total solids of urine is not far from 20 per cent, whereas with the elephant fed on hay alone it is a somewhat lower percentage. On at least three days with Jap, however, the percentage was above 20, so that in all probability it may be accepted as a general rule that the ash represents about one-fifth of the total solids in the urine.

Organic Matter

From the energy standpoint, the organic matter in the total solids is of greatest significance, for it is through this source that potential energy is lost. Obviously the organic matter in the urine is represented by the difference between the total solids and the ash. On the average, the organic matter amounted to 81 per cent of the total solids in the urines of Jap and to 78 per cent in the urines of the Barnes herd.

In striking an energy balance, every available source of information must be employed to note the intake or output of energy. Hence organic matter in the urine is a definite factor. The organic matter is made up in large part of carbon. Consequently the carbon determination itself should be fairly closely associated with organic matter. The ratio of organic matter to nitrogen and the ratio of carbon to nitrogen in urine have long been studied in problems with domestic animals. They will be treated more in detail after consideration of the nitrogen in the urine, but the relationships between the organic matter and the nitrogen given in table 32 for Jap and in table 33 for the Barnes herd show a striking variability. Thus with Jap these ratios are very wide, ranging from 6.7 to 9.6, with an average of 8.0 mg. of organic matter for each milligram of nitrogen. But with the Barnes herd the ratios are only about half of this, averaging 4.5 mg. of organic matter for each milligram of nitrogen. Furthermore, the lowest ratio found with Jap, 6.7, is considerably higher than the highest ratio found with any of the individual elephants in the Barnes herd, that is, 5.9. This difference is to be explained again by the wide difference in the two types of feed received by the elephants, a difference in feed which undoubtedly will be found to play a rôle in all the comparisons between Jap and the Barnes herd. These relations, however, can better be discussed when a direct comparison is made of the nitrogen-carbon ratios and the nitrogen-energy ratios. (See page 227.)

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[1] Benedict, F. G., Carnegie Inst. Wash. Pub. No. 203, 1915, table 24, p. 239.

[2] Benedict, F. G., Carnegie Inst. Wash. Pub. No. 77, 1907, p. 355.

NITROGEN

Nitrogen per cubic centimeter of urine—No one chemical element is of more importance in urine analyses than the total nitrogen. As seen by reference to tables 30 and 31, this factor was determined in all the urine samples analyzed and has been expressed as milligrams of nitrogen per cubic centimeter of urine. As a contribution to the chemistry of the urine of the elephant, this factor is of value, although it gives no direct information regarding the probable 24-hour nitrogen output, unless it can be associated with an actually determined or reasonably well approximated total volume of urine per day. These values for nitrogen excretion, as reported in tables 30 and 31, represent individual samples of urine from a large number of elephants. As is to be expected, the variability in the amount of nitrogen excreted per cubic centimeter of urine was great. The lowest nitrogen excretion was noted with Jap, namely, 0.66 mg. at 9.05 p.m. on April 2. With the Ringling, Downie, and Barnes herds there are no nitrogen values as low as those reported for Jap, for with these herds the lowest value is 1.47 mg. with No. 53 of the Barnes herd and the highest is 7.86 with No. 22 of the Ringling herd. This value for No. 22 is more than ten times greater than the minimum value noted with Jap. The results of the analyses of the composite samples of Jap's urine (see table 32), which approximate as nearly as possible 24-hour collections, are perhaps less influenced by any momentary changes in the concentration of the urine, but even in these composite samples there is a range from 2.47 to 5.86 mg. With such great variability in the urinary nitrogen excretion it is hardly wise to attempt to derive any average value representing the probable nitrogen elimination per cubic centimeter of urine. Yet if all the values noted with Jap were averaged and this average included with the individual values obtained with the elephants in the three herds, the general average would be not far from 5 mg. of nitrogen per cubic centimeter of urine. This value could be used to calculate the approximate total nitrogen output of the elephant (see page 216), which might well be as close an approximation as any estimation of the food intake, unless the food intake was measured with extraordinary precautions.

Relationship Between Nitrogen Per Cubic Centimeter and Specific Gravity of Urine

As has already been pointed out, the amounts of total solids are fairly closely associated with the specific gravity, in that the low gravities are accompanied by low amounts of total solids. Comparison of the values for specific gravity and nitrogen excretion per cubic centimeter of urine, as reported in tables 30 and 31, shows also that in general when the specific gravity is low the nitrogen per cubic centimeter is low. Thus with Jap on April 4 there are three specific gravities as low as 1.012 or under, accompanied by values for nitrogen per cubic centimeter of 1.70 mg. and under. The low gravity on April 7 at 1.35 p.m. of 1.013 is accompanied by the lowest nitrogen excretion per cubic centimeter on that date. Again on April 9 the low specific gravity of 1.013 is accompanied by the lowest nitrogen excretion on that date. On April 10 there are two very low gravities and two low nitrogen values for the same urine samples. With none of the elephants are there high specific gravities that are not accompanied by a relatively high nitrogen output. It would seem as if there is an approximate relationship between these two factors.

To study this point more critically, the results obtained on the individual samples of Jap's urine in March and April and on the individual samples from the three herds of elephants have been plotted in figure 12, the ordinates representing the specific gravities and the abscissæ the nitrogen excretion per cubic centimeter. The data secured with Jap are indicated by solid dots. Those obtained with the Ringling herd are indicated by hollow circles, those with the Downie herd by hollow triangles, and those with the Barnes herd by crosses. This chart shows at a glance that there is a wide variability in both the specific gravities and the nitrogen per cubic centimeter with different elephants, and as a large number of the plotted values are for the individual elephant, Jap, this variability likewise applies to the individual. But in general it is true that the higher the nitrogen excretion the higher the specific gravity. There are, however, occasional exceptions, for example, the fairly high specific gravity of 1.020 accompanied by a low nitrogen value of 1.32 mg. From an examination of the individual points on this chart it is seen that for the same number of milligrams of nitrogen, Jap has, on the whole, a specific gravity higher than the gravities of the other elephants. At the other extreme are the series of crosses representing the Barnes herd, which show for the same number of milligrams of nitrogen an unusually low specific gravity. This comparison suggests that there was a higher proportion of non-nitrogenous material in Jap's urine, and consequently one would expect higher carbon to nitrogen and calorie to nitrogen ratios. This is borne out by subsequent determinations, in which these ratios were especially studied. (See page 225.) These findings, in all probability, reflect the differ-

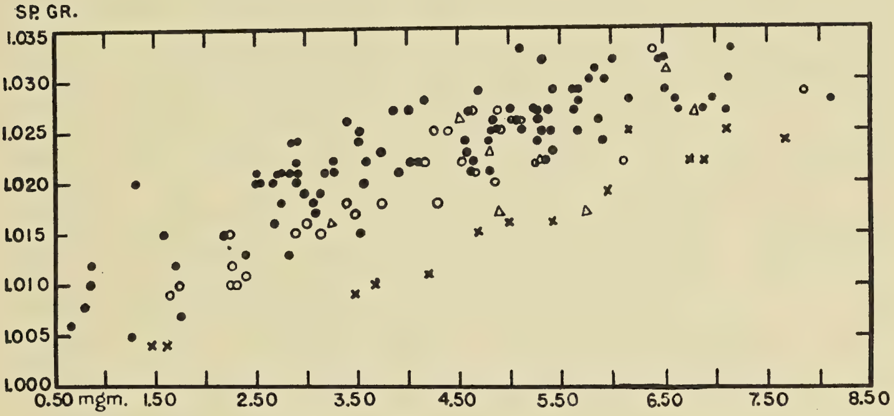

FIG. 12—RELATIONSHIP BETWEEN SPECIFIC GRAVITY AND NITROGEN PER CUBIC CENTIMETER OF URINE.

The data for Jap are indicated by solid dots, for the Ringling herd by hollow circles, for the Downie herd by hollow triangles, and for the Barnes herd by crosses.

ences in the character of the feed, Jap receiving exclusively hay and the Barnes herd hay with a larger proportion of concentrates than that in the rations of the other herds. However, in these comparisons one should constantly bear in mind that these relationships are based in one instance upon data for only one animal and in the other instances upon data for several different animals. It is clear that no general curve can be drawn through the plotted data in figure 12 to show the average relationship between the nitrogen excretion in urine and the specific gravity.

Twenty-Four Hour Excretion of Nitrogen

In the absence of 24-hour collections of urine from the several elephants for which individual specimens of urine were analyzed, a rough calculation of the probable total nitrogen output per day may be made in the following manner, although perhaps based upon too many assumptions. The probable average 24-hour discharge of urine by Jap has been calculated to be 50 liters. (See page 204.) Per kilogram of body weight, this amounts to 13.6 cc. The fact that the other elephants were studied at a different season of the year than was Jap and that there were undoubtedly differences in the amounts of water drunk affects the calculations for these animals greatly. Yet if the assumption is made that the volume of urinary discharge is proportional to the body weight, namely, 13.6 cc. per kilogram of weight, the probable total volume of urine voided by each of the several elephants studied can be calculated from their body weights. The total volumes thus obtained can be multiplied by the values for milligrams of nitrogen per cubic centimeter of urine, as determined in at least one sample of urine from each elephant, to approximate the total 24-hour excretion of nitrogen—or the average value of 5 mg. of nitrogen per cubic centimeter of urine (based upon the urine analyses for all the animals—see page 214) can be used. One of the criticisms against this method of calculation is that one specimen of urine from an elephant can hardly be accepted as typical of the composition of the urinary output of that animal for the entire day unless that specimen happens to have a specific gravity much in line with the gravities (1.023) noted with the urines of Jap (urines which contained, on the average, 4.5 mg. of nitrogen per cc.). Although large animals will obviously void a larger volume of urine than smaller animals, at best the calculation of the probable 24-hour nitrogen output as outlined above can be only crude—still much better than that computed from the approximate food intake of any one animal.

This type of calculation, based upon the supposition of uniformity in the urinary discharge in proportion to the body weight, finds its severest test when applied to the large number of urinary nitrogen determinations made for Jap. Since the nitrogen output per cubic centimeter of urine in her case varied from 0.66 to 8.12 mg., application of such varying values to the computed total volume of urinary discharge would be out of the question. On the other hand, if a large number of determinations of this type had been made and the average value were employed, the probable daily output of nitrogen could be computed with a fair degree of accuracy. Since with all the elephants except Jap the urinary nitrogen determinations were confined to one or at the most two specimens, such a calculation is not justified.

The estimated average of 5 mg. of nitrogen per cubic centimeter of urine (see page 214) has its greatest interest when applied to a known volume of urine per 24 hours, when that is satisfactorily collected. Only in the case of Jap can the total 24-hour volume of urine even be approximated, and even in this case there were no complete 24-hour collections. From the records of the total volume of the samples collected consecutively without any loss of urine, from the total time represented by these collections (time from last incomplete collection to time of last consecutive complete collection), and from the nitrogen analyses of these samples, an attempt has been made to compute the average daily nitrogen output of Jap during the nine days of the digestion study in April. These calculations are based upon periods ranging in length from as short as 1 hour and 7 minutes (from 5.39 p.m. to 6.46 p.m. on April 4) to as long as 12 hours and 53 minutes (from 9.15 a.m. to 10.08 p.m. on April 10) and 16 hours and 28 minutes (from 1.18 p.m. on April 5 to 5.46 a.m. on April 6). Obviously much greater weight should be laid upon the longer periods than upon the shorter. Nevertheless the calculations have been made for all periods of complete collection, regardless of length, and the results are recorded in table 34. It is clearly recognized that a value based upon a short period of collection can be applied to a 24-hour period only with considerable reserve, for this assumes that the voiding was complete and that there was no retention in the bladder. It is possible that the elephant, if frightened or aroused, might retain some of its urine at the time of voiding. Unlike the elephant, most animals eat during only half of the day and in their cases it is easy to understand that a 24-hour period of collection is necessary if the normal daily rhythm of nitrogen excretion is to be accurately studied. The elephant presents the unique situation of an animal that is almost constantly eating. Hence the intake of nitrogen is essentially constant from hour to hour, and the collection in 24-hour periods is not so imperative as when there is a daily rhythm in the intake.

According to the data in table 34 the estimated 24-hour nitrogen excretion was 130 grams on April 2 and 161 grams on April 3. These two estimates are more divergent than any of the others in the entire series, for beginning with April 4 the calculated values are reasonably uniform, the minimum being 204 gm. (based on a period of 2 hours and 51 minutes) and the maximum 328 gm. (based on a period of 3 hours and 59 minutes). In the two longest periods of collection, each amounting to more than twelve hours, there is singular agreement between the results, 235 grams on April 5 and 230 grams on April 10. Averaging of these estimates is questionable, because of the three low values at the beginning of the series and the two high values on April 9 and 10. The average for the entire series, however, 235 grams, is in close agreement with the estimates of 235 and 230 grams for the two longest periods of collection. It is, therefore, a reasonable assumption that Jap, under the conditions of experimenting (that is, on a constant ration of hay alone), had a probable daily output of nitrogen in the urine amounting very closely to 235 grams. Since Jap weighed 3672 kg., her urinary nitrogen

TABLE 34—*Estimated volumes of urine and urinary nitrogen excreted per 24 hours—elephant Jap*

Date	Period of consecutive complete collections			Per 24 hours	
	Time of day	Duration		Volume of urine	Nitrogen excretion
1935		*hrs.*	*min.*	*liters*	*gm.*
Apr. 2......	9.05 p.m. to 11.15 p.m.	2	10	98.3	130
Apr. 3......	8.11 a.m. to 10.25 a.m.	2	14	50.7	161
Apr. 3–4....	11.06 p.m. to 2.21 a.m.	3	15	69.4	189
Apr. 4......	5.39 p.m. to 6.46 p.m.	1	7	123.6	210
Apr. 4......	7.59 p.m. to 10.50 p.m.	2	51	66.4	204
Apr. 5–6....	1.18 p.m. to 5.46 a.m.	16	28	46.9	235
Apr. 6......	8.05 a.m. to 11.36 a.m.	3	31	30.9	220
Apr. 6......	5.24 p.m. to 11.52 p.m.	6	28	40.1	246
Apr. 7......	5.35 a.m. to 8.58 a.m.	3	23	48.5	275
Apr. 7–8....	9.03 p.m. to 12.30 a.m.	3	27	73.0	272
Apr. 8......	6.54 a.m. to 8.46 a.m.	1	52	44.7	238
Apr. 8......	6.50 p.m. to 9.14 p.m.	2	24	47.3	256
Apr. 9......	2.50 a.m. to 9.26 a.m.	6	36	47.5	266
Apr. 9......	4.55 p.m. to 8.54 p.m.	3	59	92.1	328
Apr. 9–10...	11.02 p.m. to 12.19 a.m.	1	17	61.8	311
Apr. 10......	1.59 a.m. to 4.45 a.m.	2	46	46.2	261
Apr. 10......	9.15 a.m. to 10.08 p.m.	12	53	45.2	230
Apr. 11......	6.10 a.m. to 7.44 a.m.	1	34	42.8	206
Average....	....	....		59.7	235

ouput per kilogram of body weight per 24 hours would amount to 64 milligrams.

Among the animals for which urine data are available, animals fed under conditions comparable to those of the elephant, that is, chiefly hay alone, are the cows studied by Professor E. G. Ritzman at the University of New Hampshire. These cows weighed 600 kg. and were on a supposedly maintenance ration of timothy hay. With these cows experiments (unpublished) extending over many weeks showed a nitrogen excretion in the urine per kilogram of body weight per 24 hours varying from 38 mg. to as high as 125 mg. These values are not significantly different from those noted with Jap, for if the calculations in table 34 were computed to the per kilogram of body weight basis, the variability would be almost as great as with the cows. The average value for Jap, that is, 64 mg. per kilogram of body weight, as a matter of fact is higher than three of the values found in the cow experiments. Jap weighed 3672 kg. and the cows one-sixth of this, but one would not expect a direct linear relationship between size and nitrogen excretion per unit of weight. Until further data on other animals are available, however, in which quantitative 24-hour periods are used, it is somewhat idle to discuss this matter in too great detail.

It is a matter of regret that the approximation of the 24-hour output of urinary nitrogen can be made for only one elephant, Jap, an animal not working, subsisting upon a single food material (hay), and for the most part

TABLE 35—*Constituents in the urine of the elephant Jap*[1]

Period of collection of composite sample		Total nitrogen per cc. of urine	Ammonia-nitrogen		Urea-nitrogen		Amino-acid nitrogen		Allantoin per cc. of urine	Allantoin-N		Sodium chloride per cc. of urine	Total sulphur per cc. of urine	Nitrogen divided by sulphur
Date	Time		Per cc. of urine	Per cent of total nitrogen	Per cc. of urine	Per cent of total nitrogen	Per cc. of urine	Per cent of total nitrogen		Per cc. of urine	Per cent of total nitrogen			
1935		*mg.*	*mg.*		*mg.*		*mg.*		*mg.*	*mg.*		*mg.*	*mg.*	
Apr. 2– 3	1.15 p.m.– 2.10 p.m.	2.86	0.082	2.9	1.89	66.1	0.068	2.4	0.460	0.163	5.7	3.49	0.594	4.8
Apr. 3– 4	2.10 p.m.– 2.14 p.m.	2.65	.041	1.5	2.03	76.6	....	....	.419	.148	5.6	2.65	.413	6.4
Apr. 4– 5	2.14 p.m.– 1.18 p.m.	2.46	.039	1.6	1.92	78.0	.040	1.6	.428	.152	6.2	1.14	.312	7.9
Apr. 5– 6	1.18 p.m.–11.36 a.m.	5.10	.093	1.8	3.72	72.9	.054	1.1	.456	.162	3.2	2.40	.744	6.9
Apr. 6– 7	11.36 a.m.– 1.35 p.m.	5.47	.087	1.6	3.82	69.8	.074	1.4	.834	.296	5.4	3.94	.749	7.3
Apr. 7– 8	1.35 p.m.–12.10 p.m.	4.59	.047	1.0	3.36	73.2	.061	1.3	.471	.167	3.6	3.74	.582	7.9
Apr. 8– 9	12.10 p.m.–11.36 a.m.	5.59	.058	1.0	3.85	68.9	....	....	....	....	....	2.06	.523	10.7
Apr. 9–10	11.36 a.m.– 1.20 p.m.	5.85	.072	1.2	3.94	67.4	.059	1.0	.621	.220	3.8	2.88	.807	7.2
Apr. 10–11	1.20 p.m.– 5.00 p.m.	4.49	.187	1.2	3.09	68.8	....	....	....	....	....	2.48	.396	11.3
Apr. 11	5.00 p.m.–10.02 p.m.	5.23	.092	1.8	4.53	86.6	.091	1.7	.570	.202	3.9	....	.624	8.4

[1] All analyses were based on samples preserved with chloroform, thymol, and hydrochloric acid, except in the case of the sodium-chloride data, which are for samples preserved with chloroform and thymol.

under unusual conditions as regards environmental temperature. To what extent the composition of the urine would be modified by a more substantial and more varied ration (particularly richer in protein), by the superimposition of severe muscular work, and by a more equable environmental temperature can at best be only a matter for speculation. Undoubtedly a richer protein diet would result in an increased nitrogen output in the urine, but only under conditions of approximately full normal nitrogen reserve. The attempted estimations of the total nitrogen excretion of the elephant are, therefore, highly problematical and of value only in suggesting further lines of investigation.

Table 36—*Creatinine, creatine, and creatinine-N in the urine of the elephant Jap*

Date	Creatinine per cc. of urine		Creatine per cc. of urine	Preformed creatinine-N		Total creatinine-N	
	Preformed	Total		Per cc. of urine	Per cent of total nitrogen	Per cc. of urine	Per cent of total nitrogen
1935	*mg.*	*mg.*	*mg.*	*mg.*		*mg.*	
Apr. 2– 3	0.227	0.424	0.229	0.084	2.9	0.158	5.5
Apr. 3– 4	.164	.407	.282	.061	2.3	.151	5.7
Apr. 4– 5	.245	.505	.302	.091	3.7	.188	7.6
Apr. 5– 6	.477	.995	.601	.177	3.5	.370	7.3
Apr. 6– 7	.324	.663	.393	.120	2.2	.246	4.5
Apr. 7– 8	.231	.514	.328	.086	1.9	.191	4.2
Apr. 8– 9	.295	.611	.367	.110	2.0	.227	4.1
Apr. 9–10	.305	.665	.418	.113	1.9	.247	4.2
Apr. 10–11	.311	.604	.340	.116	2.6	.225	5.0
Apr. 11	.436	.901	.539	.162	3.1	.335	6.4

Partition of Nitrogen Excretion

The results of the determinations of the nitrogenous constituents in the composite samples of Jap's urines have been summarized in tables 35 and 36. The results of the few determinations of similar nature on the individual samples of urine from the elephants in the Ringling herd have been summarized in table 37.

Ammonia-nitrogen—The first point of interest in any consideration of the partition of the nitrogen excretion in the urine of Herbivora is the proportion of the total nitrogen as ammonia. Previous studies on fasting steers have shown that when the urines were properly preserved at the time of voiding, the ammonia content was relatively low.[1] The same is true with regard to the elephant. The ammonia-nitrogen content of Jap's urine, expressed in terms of the percentage of total nitrogen, is under 2 per cent except in one instance. In spite of the rather low nitrogen level at which Jap was living, this percentage is very low. With the fasting steers the values are for the most part above 2 per cent, as most of the values were between 5 and

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[1] Carpenter, T. M., Amer. Journ. Physiol., 1927, **81**, p. 519; Carpenter, T. M., Proc. Nat. Acad. Sci., 1925, **11**, p. 155; Benedict, F. G., and E. G. Ritzman, Carnegie Inst. Wash. Pub. No. 377, 1927, pp. 104 *et seq.*

TABLE 37—*Sodium chloride and urea- plus ammonia-nitrogen in urines of Ringling elephants*

(Values per cubic centimeter of urine)

Elephant No.	Sodium chloride	Urea- plus ammonia-N	Elephant No.	Sodium chloride	Urea- plus ammonia-N
	mg.	*mg.*		*mg.*	*mg.*
14	1.20	1.85	29	4.80	2.84
15	4.67	2.50	30	3.91	3.48
16	9.00	5.47	31	5.17	3.33
17	1.82	1.44	32	4.25	2.67
18	2.33	2.46	34	4.48	2.94
19	2.42	4.44	35	10.65	3.24
20	6.06	4.01	36	8.36	2.93
21	3.36	3.98	37	4.36	2.36
22	4.27	6.93	38	7.10	2.83
23	1.1	1.19	39	1.62	2.29
24	2.32	3.29	40	3.14	1.38
25	3.25	4.22	41	2.10	1.64
26	1.15	1.94	42	6.84	3.82
27	2.80	2.61	44	2.15	1.92
28	6.88	3.65			

8 per cent. Strictly speaking, however, one should not compare the urine of the fasting steer with the urine of a non-fasting elephant. From analyses of nine samples of urine collected from four types of camels at the New York Zoological Park (fed on a diet of oats and timothy hay) Smith and Silvette[1] found ammonia-nitrogen percentages that are higher than the values noted with the elephant. Two of the samples of camel's urine (those on February 28 and March 19) gave values which indicated that the urines were decomposed. Dann[2] reports that the urines of cows while at pasture (supplemented by Brewer's grains), analyzed usually within a few hours of collection, contained 3.9 per cent of total nitrogen as ammonia and that the urines of cows on pasture supplemented by meadow hay contained 0.7 per cent as ammonia-nitrogen. It would seem as if the rations of the cows on pasture and meadow hay would represent more nearly the hay rations of the elephant Jap, and in this group the percentage of ammonia-nitrogen is close to that noted with the elephant.

Urea—The percentage of total nitrogen as urea, noted in the urine samples from Jap, is high in view of the fact that Jap was supposedly on a rather low nitrogen level. The values range from 66 to 87 per cent and are, in general, higher than those found with the fasting steers. With the camels studied by Smith and Silvette the percentages of total nitrogen as urea were under 70 and for the most part over 60, that is, in general slightly lower than the values found with the elephant. In the case of the cows studied by Dann the percentages were 32.8 and 42.3, on the average, or lower than noted with the elephant.

Amino-acid nitrogen—The values for percentage of total nitrogen as amino acid are of about the same order of magnitude with Jap as those

[1] Smith, H. W., and H. Silvette, Journ. Biol. Chem., 1928, **78**, p. 409.

[2] Dann, A. T., Austral. Journ. Expt. Biol. and Med. Sci., 1933, **11**, p. 53.

found with adult steers during the fasting periods proper, not during the feeding periods.

Allantoin-nitrogen—The allantoin-nitrogen in terms of total nitrogen formed a higher percentage of Jap's urine than any other constituent except urea. Presumably purine bodies are eliminated in this form instead of as uric acid. No tests were made for uric acid in any of the elephant urines. None was found present in the steers' urines. Terroine[1] found allantoin excreted in the urine by the rat, the rabbit, the dog, the pig, and man.

Preformed creatinine nitrogen—The percentage of total nitrogen excreted in the form of preformed creatinine nitrogen is fairly uniform, ranging only from 1.9 to 3.7 per cent. These values are materially lower than those found with the fasting steers, no matter what the type of fast or the condition of feeding previous to the fast. The values with the steers, when fasting, range from a level of 5 per cent to a level of from 20 to 25 per cent on the first few days of the fast. As will be shown later on this page, this comparison indicates clearly that the creatinine output of the elephant is extremely low and different from that of most Herbivora.

Total creatinine nitrogen—When the creatine is included and an estimate is made of the percentage of nitrogen as creatinine plus creatine, the values are in general uniform from period to period. They range from 4.1 to 7.6 per cent. With the camels at the New York Zoological Park the creatinine nitrogen formed a much higher percentage of the total nitrogen. With the cows studied by Dann the percentages with the group on pasture and hay rations are a little higher than in the case of the elephant, but with the group on pasture supplemented by grains the values approach more nearly the percentages noted with the fasting steers. Apparently it is a normal condition for the elephant like other herbivorous animals, to eliminate creatine when on feed, *i.e.*, not fasting. Whether this is due to actual secretion of creatine in the urine itself or to a conversion of creatinine to creatine in the bladder before voiding can not be stated. It is not improbable that the same condition rules here as occurred with the steers and as has been found with rabbits, namely, that in alkaline urine there is always creatine. That it is due to the alkalinity of the urine is supported by the fact that with fasting steers, as the fast progressed, there was practically no elimination of creatine. In other words, as the urine became acid, the formation of creatine ceased.

Creatinine coefficient—The relationship between the total amount of preformed creatinine and the body weight of the elephant, that is, the number of milligrams of preformed creatinine per kilogram of body weight, is on the average extraordinarily low. Thus, multiplication of the estimated 24-hour urinary nitrogen excretion of Jap (235 grams) by the average percentage of total nitrogen as preformed creatinine-nitrogen (2.6), division by the factor 0.3717, and division by the body weight (3672 kg.) shows that 4.5 milligrams of preformed creatinine were excreted per kilogram of body weight. With the adult fasting steers C and D, the creatinine coefficient ranged between 21 and 27 mg. and remained relatively constant at the lower level during most of the fast.[1] The coefficients noted with steers are close to the values found with a fasting man[2] and slightly higher than those found by Palladin[3] with fasting sheep. No information is given by Smith and Silvette and by Dann regarding the body weights of the camels and cows studied by them, so it is not possible to calculate the creatinine coefficients for these animals. The cause of the low creatinine coefficient noted with the elephant may be due to extra fat. However, it would take a large amount of fat to be the sole cause of so low a creatinine coefficient.

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[1] Terroine, E. F., Champagne, M., and G. Mourot, Bull. Soc. Chim. Biol., 1933, 15, p. 203.

Endogenous metabolism—The fact that the total nitrogen in the form of urea is high, that the percentage of ammonia-nitrogen is low, and that the creatinine coefficient is low in the case of Jap's urine indicates that the elephant has an extremely low endogenous metabolism. If the nitrogen output of the elephant is assumed to be at a low level, as is suggested by the observations on Jap, then one would expect that the percentages of total nitrogen in the form of ammonia and creatinine[4] and presumably allantoin would total a greater sum than they do for Jap. In other words, the lower the nitrogen level, the lower becomes the proportion of total nitrogen in the form of urea and the greater it becomes in the form of other substances, which presumably represent the minimum endogenous values. This point is of importance in connection with the general question raised by Brody,[5] Terroine,[6] and Smuts[7] regarding the relation between the endogenous nitrogen metabolism and the basal metabolism.

Nitrogen-sulphur ratio—The nitrogen-sulphur ratios of Jap are extremely low (4.8 to 1 and 11.3 to 1). In only one group of experiments with the fasting steers were values noted as low as here found with Jap. With steer D in March 1924 the ratios on the days following the fasts were about 7 to 1. Under all other conditions they were much higher.

Hippuric acid—According to statements made by Colin[8] hippuric acid was found in the urine of the elephant by Vauquelin and Fourcroy but not by Vogel. Reference to the original articles by Vauquelin and Fourcroy[9] and by Vogel[10] shows that nothing is stated by them regarding hippuric acid but that benzoic acid is considered. It is possible that the method of analyzing urine to detect the presence of hippuric acid was not discovered until after their day, but it is singular that Colin, as late as 1888, speaks of their analyses as applying to hippuric acid. Because of the apparent uncertainty regarding this particular point, tests for hippuric acid were made in the case of Jap's urine. Hippuric acid was isolated from a composite sample made up of 100 cc. from each of five of the composite samples of urine collected between April 2 and April 11. The Roaf method described by Hawk and Bergeim[1] was employed for this purpose. The material isolated was then subjected to all the qualitative tests given by Hawk, and at the same time a comparison was made with identical tests on a sample of pure hippuric acid from the laboratory stock. The melting point of the hippuric acid isolated from the elephant's urine was 185° C. and that of the laboratory sample 186° C. All the qualitative tests responded practically alike, both those on the material isolated from the urine and those on the laboratory sample. Hence it can be stated that in the elephant's urine hippuric acid was excreted in detectable amounts.[2]

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[1] Carpenter, T. M., Amer. Journ. Physiol., 1927, **81**, p. 519; Carpenter, T. M., Proc. Nat. Acad. Sci., 1925, **11**, p. 155; Benedict, F. G., and E. G. Ritzman, Carnegie Inst. Wash. Pub. No. 377, 1927, p. 122.

[2] Benedict, F. G., Carnegie Inst. Wash. Pub. No. 203, 1915, p. 262.

[3] Palladin, A., Arch. f. d. ges. Physiol., 1924, **204**, p. 155.

[4] According to the figures given by Takamatsu (Journ. Biochem., Tokyo, 1935, **21**, table IV, p. 432), the percentage of total nitrogen as creatinine in elephant urine is extremely low, namely 0.133. Although this confirms our conclusion that the elephant has a low endogenous nitrogen metabolism, we must accept Takamatsu's results with considerable reserve, because of the apparent error in his value for urea in elephant urine, which is not in agreement with the accepted relationship between urea and total nitrogen.

[5] Brody, S., Procter, R. C., and U. S. Ashworth, Univ. Missouri, Agric. Expt. Sta. Research Bull. 220, 1934.

[6] Terroine, E. F., M. Champagne, and G. Mourot, Bull. Soc. Chim. Biol., 1933, **15**, p. 203.

[7] Smuts, D. B., Journ. Nutrition, 1935, **9**, p. 403.

[8] Colin, G., *Traité de physiologie comparée des animaux*, Paris, 1888, 3d ed., **2**, pp. 848-849.

[9] Fourcroy, A. F., and L. N. Vauquelin, Journ. Soc. d. Pharm., Paris, **1**, p. 129. (Cited by D. J. C. Reil, Arch. f. d. Physiol., Halle, 1800, **4**, p. 162.)

[10] v. Vogel, H. A., Journ. f. Chemie u. Physik, 1817, **19**, p. 156.

SODIUM CHLORIDE

As an indication of the mineral constituents of the urine other than ash, titrations for sodium chloride were carried out on all but one of the composite samples of Jap's urine and on twenty-nine individual samples of urine from the elephants in the Ringling herd. (See tables 35 and 37.) Since total 24-hour collections of urine were not made, the results have been expressed in milligrams per cubic centimeter of urine. As Jap was on a uniform diet, it is justifiable to compare the results from day to day. The variability is not great, the range being only from 1.14 to 3.94 mg. and the average 2.75 mg. With the Ringling herd the sodium chloride per cubic centimeter varies greatly, from 1.1 to 10.65 mg. The average for the herd is 4.19 mg. or considerably above that for Jap. Comparison with the determinations of specific gravity (see tables 31 and 32) indicates a fairly close relationship between the two factors, for when the specific gravity is low, the chloride content is low. In figure 13 the data for the sodium chloride per cubic centimeter of urine have been plotted with reference to the specific gravities, the results for Jap being indicated by solid circles and those for the Ringling herd by crosses. At nearly all the specific gravities the sodium-chloride values for Jap are lower than those noted with the Ringling elephants. This suggests that Jap's excretion of chlorides was low and that she was receiving a small amount of chlorides in her food. It is known that she was given no salt, and the question arises as to whether the hay that she ate furnished sufficient salts. The comparison given in figure 13 obviously disregards differences in the weights of the elephants and in the character of the food. A high specific gravity is, as already pointed out, not determined by salt content alone, although influenced by it. It is undoubtedly, in the case of Jap, materially influenced by the presence of non-nitrogenous and chlorine-free bodies.

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[1] Hawk, P. B., and O. Bergeim, *Practical physiological chemistry,* Phila., 1926, 9th ed., p. 614.

[2] Takamatsu (*loc. cit.,* pp. 436-437) succeeded in isolating 3.72 grams of crystallized hippuric acid from 27.8 liters of elephant urine, along with 25.3 grams of benzoic acid.

CARBON AND ENERGY

In striking balances of income and outgo, especially with large ruminants, it is the custom to determine the carbon in the urine. This determination also has an indirect value in that frequently the energy in the urine may readily be calculated from the carbon. Although 24-hour samples of urine were not available, nevertheless carbon was determined in the urine in a number of instances and simultaneously the energy. From these observations and from the data regarding the nitrogen, total solids, and organic matter in the same samples of urine a series of ratios can be calculated which may be of help in further work. The carbon content and the heats of combustion of all the urines were determined by means of the bomb calorimeter.[1] After the combustion was finished, the bomb was taken out of the calorimeter and the compressed gases were allowed to pass into an accurately counterpoised spirometer of about 9 liters capacity. During the passage into the spirometer, samples of the gas were drawn into mercury containers, and these were analyzed for their carbon-dioxide content. The total carbon dioxide produced during the combustion was computed from the percentage of carbon dioxide in the sample and the total volume of gas in the spirometer corrected

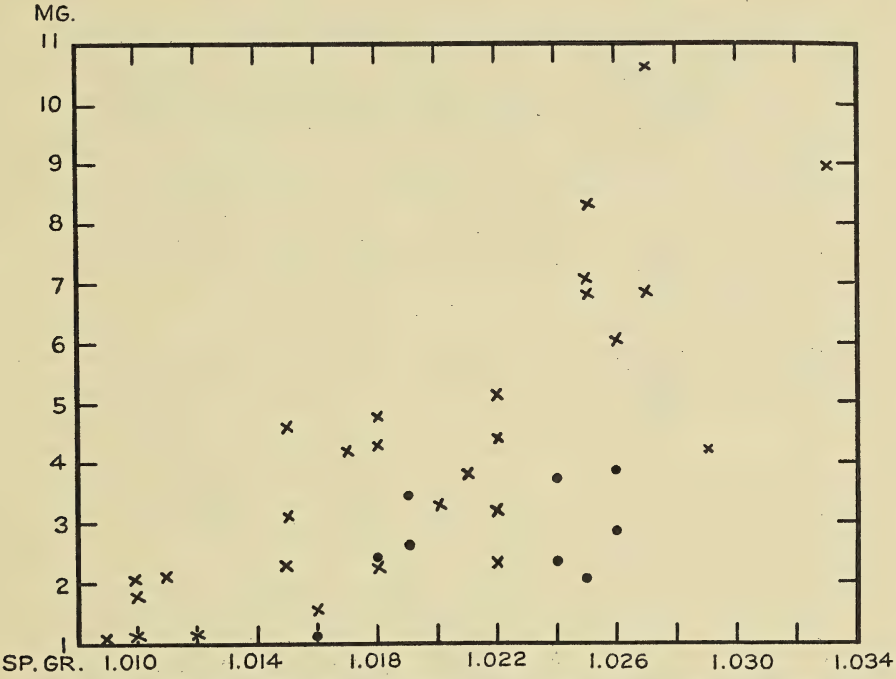

FIG. 13—RELATIONSHIP BETWEEN SPECIFIC GRAVITY AND SODIUM CHLORIDE PER CUBIC CENTIMETER OF URINE.

The data for Jap are indicated by solid circles and those for the Ringling herd by crosses.

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[1] Benedict, F. G., Abderhalden's Handb. d. biolog. Arbeitsmethoden, 1929, Abt. IV, Teil 13, p. 33.

TABLE 38—*Carbon and energy in elephant urines*

Elephant	Date	Carbon			Energy				
		Per cc. of urine	Carbon divided by total nitrogen	Carbon divided by total solids	Per cc. of urine	Calories divided by total nitrogen	Calories divided by carbon	Calories divided by total solids	Calories divided by organic matter
	1935	*mg.*			*gm.-cal.*				
Jap	Apr. 2– 3	11.5	3.9	0.327	122.4	41.6	10.7	3.50	4.33
"	Apr. 3– 4	....	....	....	103.5	38.9	....	3.22	4.07
"	Apr. 4– 5	....	....	....	85.5	34.6	....	3.29	4.48
"	Apr. 7– 8	14.5	3.2	.320	151.0	33.0	10.4	3.33	4.10
"	Apr. 9–10	18.8	3.2	.364	193.5	33.0	10.3	3.74	4.56
"	Apr. 10–11	....	....	....	130.6	29.2	....	3.50	4.23
No. 19	July 1	17.7	2.9	....	181.4	29.6	10.3	....	....
21	July 1	11.3	2.3	....	124.8	25.7	11.0	....	....
24	July 1	12.1	2.8	....	116.8	27.2	9.7	....	....
31	July 1	14.8	3.3	....	157.6	34.7	10.6	....	....
36	July 1	13.1	3.1	....	139.1	32.7	10.6	....	....
48	Aug. 1	13.3	2.2	.262	137.3	22.3	10.3	2.71	3.74
49	Aug. 1	11.0	1.63	.295	108.5	16.1	9.9	2.92	3.73
50	Aug. 1	12.5	1.76	.271	121.5	17.1	9.7	2.64	3.53
51	Aug. 1	10.3	1.74	.293	104.8	17.6	10.1	2.97	3.73
52	Aug. 1	18.3	2.38	.355	200.5	26.1	11.0	3.90	4.69
56	Aug. 1	8.3	1.78	.298	87.9	18.8	10.5	3.14	4.03
57	Aug. 1	5.7	1.56	.315	64.3	17.5	11.2	3.53	4.45

for the volume of gas left in the bomb itself. In all the combustions benzoic acid was used as a kindler. The results of these analyses are summarized in table 38. Some of the urines were extremely dilute, and large volumes of the specimens were not available. Although in these instances analyses were attempted, the error of determination was so great that the results are not reported. This difficulty was encountered with two samples from the Barnes herd, the specific gravities of which were under 1.010.

It has already been pointed out that the amounts of many of the urinary constituents vary greatly per cubic centimeter of urine and are closely correlated with the specific gravity. Since there was considerable variability in the specific gravities, it is not surprising that the carbon in these elephant urines ranged from 5.7 mg. per cubic centimeter in the case of one of the Barnes animals to as high as 18.8 mg. on one day with Jap. The energy in urine also depends in large part upon the density of the urine, and the results vary from 64.3 gram-calories per cubic centimeter with elephant No. 57 to 200.5 gram-calories with elephant No. 52. With these two elephants also the minimum and maximum values for carbon in urine were noted.

The ratios of carbon to nitrogen show striking differences between the Barnes herd and the other elephants. Those for Jap range from 3.2 to 3.9. The average for the Ringling herd is 2.9 and for the Barnes herd considerably lower, 1.9. This is further evidence that the urine of Jap contained a much larger proportion of non-nitrogenous materials than did the urines of the other elephants, a fact that again is associated with the striking differences in the character of the rations.

The ratios of energy to nitrogen vary from 16 to 42. With the Barnes herd the calories per gram of nitrogen are lower than those with either the Ringling herd or Jap. The values for Jap are, in general, somewhat higher than those for the Ringling elephants, a still further proof of the greater amount of non-nitrogenous, organic material in Jap's urine. It is the custom in experiments with many domestic animals to calculate the calories in urine on the basis that the energy content of the urine will be about 25 calories per gram of nitrogen. One might look for the establishment of a corresponding value in the case of the elephant. But the variability in the ratios is so great that one would hardly be justified in drawing an average that could be used to calculate from the nitrogen the calories in urine, for even with the Ringling and the Barnes herds there is a pronounced difference in the results, those for the Barnes herd being only about two-thirds those for the Ringling herd. The differences in these ratios are ascribable again, without doubt, to the character of the rations.

Since the energy in urine is closely associated with its carbon content rather than its nitrogenous material, the calculation of the calories per gram of carbon has special interest. On this basis the values for all the elephants closely approximate 10, and it is clear that if one knows the carbon in the urine, the energy in urine can be calculated with reasonable accuracy by multiplying the carbon value by 10.

Since the determination of the carbon presents considerable difficulty, the ratios between the carbon and the total solids in these urines were also calculated, as of some significance. From these the inference is that for each gram of total solids 0.3 gram of carbon may be expected. For every gram of total solids excreted the urines of the Barnes herd had an average energy value of 3.1 large calories and those of Jap 3.4 large calories. Since the determination of the total solids is relatively simple, this ratio has a practical value and, without undue weight being ascribed to the values for Jap, it can be stated that the average value for all the elephants would be about 3.2 large calories per gram of total solids. Because in the total solids the organic matter alone contributes toward heat, the ratio between the calories in urine and the organic matter should be found to be even closer than that between calories and total solids. Thus it is seen that for every gram of organic matter there were approximately 4 calories in the urines of the Barnes herd and 4.3 in the urines of Jap. The deviations are relatively so small that it can be considered that the energy value of the urine of the elephant, in general, is 4 calories per gram of organic matter. These ratios of energy to total solids and to organic matter, although by no means replacing actual determinations of carbon or energy in urine, are reasonably close approximations to what may be expected with normal elephant urine, and consequently may serve for approximate calculations of the energy and the carbon in urine in which the total solids and particularly the organic matter have been determined.

NITROGEN BALANCE

An animal in a well-nourished condition and on maintenance rations is supposed to be given enough food to prevent drafts upon body material. This applies equally as well to the protein as to the calories, for a diet sufficient in calories may still be deficient in protein. It was suspected from the start that since Jap was fed hay only, there might have been a deficiency in her protein intake and a consequent draft upon body material. From the data derived from the incomplete collections of urine, the at best not perfect sampling of hay, and the complete collection of feces during the 9-day digestion period in April, a highly probable estimate can be made of Jap's nitrogen balance. As has been shown in table 29, the total nitrogen intake in the hay during this 9-day period amounted to 4.68 kg. and the total nitrogen outgo in feces to 2.42 kg. It has been estimated (see table 34) that the nitrogen excretion in the urine was 235 grams per day. The probable excretion for nine days was, therefore, 2.12 kg. The possibility of the loss of nitrogen in the scurf and the hair (which was taken into account in the meticulous experiments of Armsby[1]) will be disregarded. Thus, the total nitrogen output can be considered to have been 4.54 kg. Hence there was a slightly positive nitrogen balance of 0.14 kg. during the nine days or 140 grams, which corresponds to 15.5 grams per day. If this is converted into terms of protein by use of the factor 6.25, it can be seen that there was a storage of 97 grams of protein per day. Since Jap was the equivalent in body weight of sixty men, each weighing 60 kg., this would be the equivalent with man of a storage of about 1.5 grams of protein per day or 0.25 gram of nitrogen.

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[1] Armsby, H. P., *The nutrition of farm animals,* New York, 1917, p. 203.

In the defective method of calculation of the urinary nitrogen excretion per 24 hours (see table 34) values on two days as low as 130 and 161 grams of nitrogen were found and on other days of over 300 grams. These results are derived from incomplete 24-hour collections of urine. By any method of calculation, however, it is reasonably certain that the nitrogen intake of Jap was not seriously deficient, and she might perhaps be considered to have been very closely in nitrogen equilibrium. It is striking that an animal of the size of Jap, having such imperfect digestibility, could subsist for so many weeks, if not months, on such a protein-poor ration and yet not show a definite nitrogen deficiency. It is the common belief that in wintering cattle it is next to impossible to secure nitrogen equilibrium on hay alone, and that a supplement of some kind of concentrate is necessary. It is of special significance that Jap did not have a marked nitrogen loss, for on this basis it can be assumed that she was in a reasonably normal state when the special study of the gaseous metabolism and the energy output was made. If she had been on a definitely low nitrogen level, it could be argued that her energy output was pronouncedly affected by the low protein intake.

There still remains the possibility that prior to our beginning work with Jap she may have been sufficiently long on a reduced ration to remove a considerable amount of the labile nitrogen that she may have had. Our data do not show this. On the other hand, the fact that the data obtained in the 9-day digestion experiment indicate she was nearly in nitrogen equilibrium is reasonable proof that her storage of nitrogen had not been seriously depleted prior to our tests.

SODIUM-CHLORIDE BALANCE

Calculation of the sodium-chloride balance in the case of Jap has peculiar interest. Although this does not take into account all the salts, nevertheless it is a factor that is included as one of the routine measurements with many animals when definite amounts of sodium chloride are fed. Since Jap was given no salt, the sodium chloride excreted must have come from the hay and water alone or, if the balance proves to be negative, in part from drafts upon previously stored salt in the tissues.[1] From the analyses of the water, hay, feces, and urine of Jap during the 9-day digestion experiment it is possible to compute the probable sodium-chloride balance. In the drinking water she obtained only about 1.5 grams of sodium chloride per day. (See page 176.) The total weight of hay, as eaten, during the 9-day digestion trial amounted to 449 kg. (see page 163), and since this hay contained 3.61 mg. of sodium chloride per gram of air-dry matter (that is, as fed), 180 grams of sodium chloride were obtained per day in the hay that was eaten. The total weight of dry feces during the nine days was 232 kg. (see page 195), and since they contained 1.48 mg. of sodium chloride per gram of dry matter, the total daily excretion of sodium chloride in feces amounted to 38 grams. The urinary nitrogen excretion per day averaged 235 grams. (See page 218.) The ratio of sodium chloride per cubic centimeter of urine to total nitrogen per cubic centimeter of urine was 1:1.5. Hence the daily excretion of this salt in the urine was 157 grams. The total daily intake was, therefore, 181 grams and the total daily excretion 195 grams. This indicates a seeming loss of 14 grams of sodium chloride per day.

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[1] With humans, even when fasting, chlorides are excreted in the urine (Benedict, F. G., Carnegie Inst. Wash. Pub. No. 203, 1915, p. 269).

Armsby [1] has reported that 2.5 kg. of meadow hay contained 17 grams of chlorine. Jap ate daily 50 kg. of hay or twenty times this amount. Had she eaten the meadow hay mentioned by Armsby, therefore, she would have received 340 grams of chlorine, corresponding to essentially 560 grams of sodium chloride or somewhat over three times that in the hay she actually ate. It appears, therefore, that Jap was not only deprived of sodium chloride in the form of salt but was fed hay extraordinarily low in chlorine.

One of the finest specimens of exhibition elephant with which we have come in contact is "Big Rosie" (weight about 8500 pounds), who at present (December 1935) is being used in a New York spectacle. She gives every evidence of having received unusual care, with special efforts to give her adequate feed. Her keeper reported that in the three years he has had charge of her she has never been fed salt as such. He stated that when hay is baled, salt is frequently put into it to aid in drying and keeping it. This salt, together with that normally existing in the hay fiber itself, was considered sufficient for "Big Rosie." Perhaps American hay has one good quality that is not characteristic of Indian succulent feed, namely, that its salt content is such that no extra salt in the diet is needed. In India salt *per se* is fed to the elephant, and it is stipulated that so much salt per week should be given. In the United States apparently there is no need for the extra salt, since the hay itself contains enough salt in two forms, (1) as salt in the grass itself, and (2) the salt occasionally added in baling.

Obviously this whole matter of salt study needs revision, based on analyses of actual *24-hour* specimens. These were not obtained with Jap and the other elephants. The general picture, however, suggests that Jap was in essentially sodium-chloride equilibrium. For the normal maintenance of an animal, so far as body fluids are concerned, it is essential that the salt intake should be adequate, for the presence of salt in the blood is intimately bound up with the general equilibrium of the constituents in the blood. That the body will protect itself from the withdrawal of salt is shown by results obtained with the fasting steers.[2] With these animals the chloride excretion gradually decreased until there was practically no elimination, and subsequently the elimination began again. This was interpreted as due to the fact that at first the steer was holding on to the salt so as to maintain the proper equilibrium in the blood and the subsequent increased elimination represented the actual destruction of tissues and fluids, with consequent elimination of the chloride in them. The rather narrow borderline of salt balance noted with the elephant Jap shows that the practise of elephant men in feeding (along with hay) definite amounts of salt from time to time is thoroughly justified. Salt should be a definite ingredient in the elephant's rations, a factor recognized for many years in feeding the large captive herds in India.

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[1] Armsby, H. P., *The nutrition of farm animals,* New York, 1917, p. 333.

[2] Carpenter, T. M., Amer. Journ. Physiol., 1927, 81, p. 519.

WATER BALANCE

From the data obtained during the 9-day digestion experiment with Jap regarding the daily amounts of water and hay consumed and the daily excretion of urine and feces, and from the observations on the water vaporized from the lungs and the skin (subsequently to be discussed—see page 273), the water balance of this elephant can be calculated with reasonable accuracy. Thus, the intake of water per 24 hours was, on the average, 139 kg. From the average amount of hay eaten daily and the analysis of its moisture content, it is calculated that there was an additional intake of water from this source amounting to 4.0 kg. The average daily water intake was, therefore, 143.0 kg. The total daily excretion of urine has been calculated (in the absence of complete 24-hour collections) to have been 50 liters or (since the specific gravity averaged 1.023) 51 kg. Deduction for the total solids in the urine (2.2 kg. daily) leaves for water in the urine 48.8 kg. Complete collections of feces were made, and the only error here is whether the 9-day digestion period was long enough to secure an average output of feces corresponding to the food intake. The moisture content of the fresh feces was 77 per cent, and 108.9 kg. of fresh feces were passed daily. Hence the water in the feces amounted to 83.8 kg. per day. For the data regarding the water vaporized from the lungs and the skin reference must be made to table 43, page 274, from which it can be seen that on the average, in two days of experimenting, Jap excreted 22.2 kg. of water daily through the lungs and the skin. Thus the total daily output of water was 154.8 kg. as compared with a total daily intake of 143 kg. This indicates a negative water balance of 11.8 kg. per day.

From these calculations it is concluded that Jap was approximately in water equilibrium. The modern attempts at ultra-refinement of the calculation of the water balance in accordance with the nature of the food metabolized[1] can not be approximated in the computations for the elephant Jap, owing to the necessity for a number of assumptions regarding intake and outgo.

GASEOUS METABOLISM

The most intricate physiological measurement with an animal of the size of the elephant is the measurement of the total gaseous metabolism, namely, the complete oxygen consumption, the complete carbon-dioxide elimination, the complete methane exhalation, the respiratory quotient, and the water vaporized from lungs and skin. Because of the complexity of applying gaseous metabolism technique to an animal of such enormous size, the total gaseous exchange of the elephant has not heretofore been investigated. A study of the respiratory exchange from the lungs of the elephant is theoretically possible, by connecting the animal's trunk with a mask or tube and collecting the expired air from the trunk. In such trunk-respiration experiments, especially if the trunk is connected with a spirometer, records can be secured with regard to the respiration rate, an approximate idea can be obtained of the total volume of air exhaled from the lungs, and the presence or absence of methane in expired air can be demonstrated. But as will be discussed later (see page 235), one can not be sure of thus measuring the entire products of respiratory exchange. To determine the entire gaseous metabolism of the elephant a chamber method is imperative, whereby measurements can be made not only of the products of normal respiration through the trunk but also of any possible interchange of respiratory gases through the mouth and especially (as a result of extensive fermentations) of the relatively large amounts of methane given off through the anus. Our plan for studying the gaseous metabolism of the elephant, therefore, although including a study of the trunk respiration, was based primarily upon the chamber method.

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[1] Newburgh, L. H., Johnston, M. W., and M. Falcon-Lesses, Journ. Clin. Invest., 1930, 8, p. 161; Newburgh, L. H., and M. W. Johnston, *The exchange of energy between man and the environment*, Baltimore, 1930, pp. 84 *et seq.;* Peters, J. P., *Body water, The exchange of fluids in man*, Baltimore, 1935, pp. 169 *et seq.*

The study of the respiratory exchange has several definite objects, first, to give information with regard to the chemistry of the respiratory gases, particularly the carbon-dioxide excretion, the oxygen consumption, and the methane production. From the measurements of these three gases many computations can be made, for example, of the amount of carbon dioxide attributable to methane, the apparent respiratory quotient, and the true respiratory quotient. The most important use of the respiratory exchange study, however, is (in lieu of direct calorimetric measurements) to have a basis for the calculation of the heat production of the animal. Since oxygen as such does not enter, in significant amounts at least, into fermentative processes, the measurement of the oxygen consumption can be taken as an index of the total heat production of the animal.

Conditions Under Which Measurements Were Made

A most important object in measuring the gaseous exchange of the elephant was to secure information regarding its basal metabolism for comparison with basal metabolism measurements on other animals. For this purpose it was desirable to have the elephant in the post-absorptive condition, that is, when the active processes of digestion had ceased, and lying with, in so far as possible, complete muscular repose. Several factors, however, precluded the measurements under strictly basal conditions.

Digestive activity—In attempts to compare the basal metabolism of different animals, the greatest variant encountered, next to muscular activity, is the digestive activity. The introduction of food into the intestinal tract of an animal results in an increased metabolism. This increase is probably not caused to any considerable extent by the mechanical factor of the movement of food and undigested material along the intestinal tract but by chemical stimuli resulting from the disintegration products of the more highly complex molecules in the food. Without any increase in external physical activity, the ingestion of food may, with steers, result in an increase in metabolism of from 40 to 50 per cent by these processes incidental to digestion. Consequently in comparing the metabolism of various animals, it is important either to standardize the effect of digestion (which of itself is practically impossible to do) or, what is simpler, to withhold food for several hours or, in certain cases, days. Under these conditions food has no direct effect, and this complicating factor is thus eliminated.

The withdrawal of food from animals like the mouse, cat, dog, rabbit, guinea-pig, and even man presents no great problem. When it was first proposed to withdraw food from an animal like the steer, this was pronounced even by some of the best experts in animal nutrition in America as being an unwise procedure. Nevertheless two steers at the University of New Hampshire were made to fast for fourteen days[1] and there was not the slightest indication of any damage done thereby. However, in this case the animals belonged to the experimenters and any hazards were assumed by them. Although most of the elephants that are the property of show men are at times given very poor feed, both in quality and quantity, any proposition to withdraw food from them completely for even 24 to 48 hours is instantly interpreted as "dangerous" to an expensive animal and, therefore, is not permitted. Since the elephant may represent an expenditure of a thousand or more dollars, it is not surprising that the owner is disinclined to take such a risk, at least for the modest sum that any research workers could afford to pay for the use of such an animal.

Moreover, a close study of the food habits of elephants (see page 67) showed that they have a seemingly insatiable appetite and eat hay almost incessantly throughout the twenty-four hours of the day. This continuous eating by the elephant suggests that it would be especially trying to eliminate the digestive processes. Elephants are apparently very dependent upon the feeling of satiety produced by a fairly large bulk of food in their enormous stomachs, and unless food is given frequently, they become irritable and restless. This irritability and restlessness result in increased body movements, which in turn cause an increase in heat production perhaps greater than the probable extra heat production incidental to the digestive processes. Hence in attempting to avoid, on the one hand, the Scylla of digestive activity, one smashes completely upon the Charybdis of superimposed muscular activity due to the discomfort resulting from the withholding of food. Thus it appeared that even had the owners not been disinclined to submit their elephants to what they feared might be a dangerous fast and had given permission for such a fast, the animal itself would have defeated our ends by its greater irritability and consequently greater muscular movements.

This is precisely what occurred with Jap on one or two occasions, especially during the second series of observations at Campgaw, when she was not fed as frequently as she wished. She became almost frantically restless, moved from side to side, turned not a little, trumpeted, and gave every evidence of extreme discomfort and irritability. Not infrequently the attendants thought she would "pull her stakes." At night when the keeper was sleeping and Jap became hungry, she would gather up refuse from the floor and throw it at his cot to wake him to go and get hay. If this did not waken him, she would search around until she found a stone. On several occasions stones as large as a hen's egg were removed from his bed, where she had thrown them. One night she actually did pull her stakes, crashed through the doors of the barn, went immediately to another building 150 meters away where she knew hay was stored, ate what hay she wanted, and returned to the barn. These actions were evidently prompted by an intense urge for food rather than by any viciousness to destroy for destruction's sake.

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[1] Benedict, F. G., and E. G. Ritzman, Carnegie Inst. Wash. Pub. No. 377, 1927.

At the time of this investigation, therefore, it was apparent that the measurement of the basal metabolism of the elephant in the true post-absorptive condition was impracticable, although by no means impossible. Hence food was not removed from Jap before the respiration experiments but, as a matter of fact, to aid in avoiding restlessness, she was allowed to eat a small amount of food (sugar in the trunk-breathing experiments and hay and bread in the chamber experiments) during the respiration experiments themselves.

In metabolism studies on other animals, such as the cow, the steer, and particularly the horse, which subsist chiefly upon hay as does the elephant, it has been possible to withhold food completely for days and by comparing the heat production on feed and after fasting for several days to make a fairly close approximation as to the increase in heat production due to the taking of food. With the elephant the only practical procedure is to measure its total heat production while on feed and, based upon previous experience with these other animals, to apply to its measured heat production an approximate correction (in the nature of a percentage reduction) for the probable effect of digestion. The result should represent the probable post-absorptive metabolism of the elephant. This again illustrates the point that studies in comparative physiology are of inestimable value in studying the physiology of any individual species.

It is highly doubtful whether an elephant could be kept without food long enough even to approximate the post-absorptive condition, although two methods toward this end suggest themselves. An elephant while still young could be subjected to repeated, enforced fasts, at first of short and then of longer duration, and thus be gradually trained to undergo periodic fasts of from two to three days in length. Surely the enormous reserve in the elephant's body would not be heavily drawn upon during two or three days of fasting. In fact, it has been the experience of the Nutrition Laboratory that practically all animals can withstand relatively long fasts without damage, the only exception being small animals like the mouse, which withstand fasting very poorly. It is possible to train an animal thus to fasting from early youth, but this training would require considerable time and expense and hence would be impracticable. A second method would be to enforce fasting upon an adult elephant by chaining it down and withholding food for two or three days. An adult animal could undoubtedly finally be trained to submit to these harmless fasts and become used to the situation, and thus would develop into a wonderful experimental animal. However, it is highly probable that the intense urge for food would always be such as to result in a tremendous amount of muscular activity, irritability, and discomfort, which would militate against any basal metabolism measurements.

Body position—For purposes of comparison with other animals it was hoped to measure the metabolism of the elephant while lying. Elephants can be made to lie down and thus temporarily relieve the legs of the effort of supporting the body. But in this position they are under a strain,[1] are continually aware of the restraining influence of the keeper, and hence, unless normally sleeping, are by no means comparable to animals such as the horse or the cow in a stall, that are lying quietly. Furthermore, as has been found in studying large ruminants in the lying position, it is necessary to wait for some time *after* the lying position has been assumed before the measurements are begun, in order not to include the considerable muscular effort involved in the change of body position. It soon became apparent, however, that Jap could not be persuaded to lie down during the day (probably because of the last-minute change in keepers), much less remain lying until the effect of the muscular effort of changing the body position had worn off. At first sight this was a great disadvantage, but fortunately the influence of body position upon the metabolism has been so accurately measured on such a large number of animals that a reasonably close correction can be made for the effect of standing upon the metabolism. (See page 278.)

Sleep—It was also hoped to measure the metabolism of the elephant while asleep. As has already been pointed out (see page 68), however, the elephant so seldom sleeps that it is impossible to predict when the period of lying asleep will occur and especially how long it will last.

Keeper inside chamber—Another factor complicating the measurement of the metabolism of the elephant was the necessity for having the keeper inside the respiration chamber. Elephants are rarely left alone, even when well chained and hobbled. It would be hazardous to put an animal of this size, without a keeper, inside a chamber of fragile construction and attempt to control the animal from the outside through a glass window in the door. The probable basal heat production of the keeper can be computed with a high degree of accuracy, however, from his known body weight, with correction for the few muscular movements engaged in while he was sitting quietly in a chair, reading.

The gaseous metabolism measurements on Jap were, therefore, made with the animal in the standing position, while the active processes of digestion were going on and, to some extent, while the animal was actually eating. The correction of the metabolism measurements for the effects of standing and digestive activity and for the presence of the keeper inside the chamber will be explained subsequently. (See pages 266 and 280.)

Trunk-Breathing Experiments

ARGUMENTS FOR AND AGAINST MOUTH BREATHING BY THE ELEPHANT

Respiration experiments on the lower animals, especially the smaller ones, are usually made with a respiration chamber technique, though in some instances special breathing appliances have been employed. Thus, the tracheal cannula has been used frequently with rabbits and dogs and especially with large animals such as the horse, by Zuntz and his associates. Successful applications of masks covering the mouth and the nose have also been made with dogs and with goats, and Brody has even employed this method with large domestic animals. The elephant is so constituted anatomically that the nose, that is, the trunk openings and the mouth opening are farther apart than is the case with any other animal. Consequently no mask can conceivably be fitted over both of these openings. But since most animals at rest usually breathe almost exclusively through the nose and have the mouth closed, it would appear at first sight that the respiratory exchange of the elephant could be measured by means of a breathing appliance attached to the end of the trunk. The only efforts ever made to study the gaseous metabolism of the elephant by means of a breathing appliance were those of Brody, who placed a tube over the trunk. In our comprehensive program for studying the physiology of the elephant, trunk-breathing experiments were likewise included. Before one can use the results of such experiments as a measure of the total metabolism, however, it is necessary to note whether the elephant breathes exclusively through the trunk or whether air is also inhaled and exhaled through the mouth. This question likewise presents itself in the study of the physiology of respiration. If there is no mouth breathing, the technique of using a breathing appliance on the trunk alone is without criticism. If mouth breathing is possible and if the attachment of an appliance to the trunk tends to inhibit respiration through the trunk, one would expect the maximum amount of mouth breathing. Under such conditions obviously the technique of trunk-breathing experiments is fundamentally wrong.

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[1] See discussion of the heart rate in the standing and lying positions, page 134.

Examination of the earlier literature shows strikingly discordant statements regarding the elephant's technique of respiration. The preponderance of evidence, however, is to the effect that this animal breathes exclusively through the trunk. Perhaps one of the earliest comments on this subject, fantastic to be sure, is the story reported by the elder Pliny concerning the difficulties experienced by the elephant because of the python, which is reputed to crawl into its trunk and suffocate it. Since there are two openings in the elephant's trunk, the python must have crawled head first into one and backed into the other, an unlikely procedure. Nevertheless the story implies that the breathing is exclusively through the trunk and that the elephant can not breathe through the mouth. The story is cited simply as of historic and legendary interest. Many other equally fantastic legends contribute to this belief of exclusive trunk breathing, notably the classic story repeated to all children regarding the long memory of the elephant. An elephant passing through a street stuck its trunk inquisitively into a tailor's window. The tailor pricked the trunk with a needle. Some months, if not years, later the elephant (according to the legend) went through the street again, recognized the locality, filled its trunk with muddy water, and passing by the window of the tailor, discharged the water into his face. This assumes that in carrying the load of water in the trunk for some distance, the elephant must have breathed through the mouth. Obviously both legends are without any scientific foundation of fact.

One would expect the most accurate observations on this point from men who are continually handling elephants. With them the general impression is that the elephant breathes exclusively through the trunk. A few think it can breathe through the mouth. Dr. C. V. Noback, of the New York Zoological Park, is of the opinion that simultaneous expiration through the trunk and mouth can not occur, and Neuffer at the Benson Animal Farm in Nashua, New Hampshire, is of the same opinion. Clark, at the Boston Zoological Garden, argues that elephants must breathe through the mouth while drinking water. This, however, is not necessarily a proof of mouth breathing, for the time required to suck up the water into the trunk and then blow it into the mouth is relatively so short, 4 seconds (see page 174), that the elephant could easily hold the breath during that length of time. Some of the early anatomical studies lead to the conclusion that the oral cavity is completely shut-off during breathing. Further evidence against any breathing through the mouth is the fact that it is difficult to hold the end of the elephant's trunk closed by the hand, for the animal will, after a short time, insist upon pulling it away.

Direct positive evidence of the exhalation of air from the mouth can be obtained perhaps best on a cold, frosty morning. The one or two elephant men who have had the temerity to take their animals outdoors in cold winter weather (most elephant men will not subject their animals to freezing temperatures) report that not infrequently they have seen exhalations of condensed vapor from the mouth. Another certain test would be to note on the hand whether there is any discharge of air from the mouth. Three or more of the Ringling elephants had been trained to "speak." When the trunk was held in the air and the animals were commanded to speak, sounds issued from the throat and strong blasts of air were felt against the hand held at the open mouth. This experience furnished evidence that air can be expelled in considerable amounts from the mouth. In this connection Watson's statement[1] (see page 11) is also of interest.

The breathing of the elephant has frequently been compared to that of the horse and the ass, for it is well known that the horse resents greatly having its nostrils held and does not breathe easily save through the nose. Nevertheless there is proof that both the horse and the ass can exhale through the mouth in the fact that the neighing of the horse and the braying of the ass take place with the mouths open.[2] If enough air can be discharged through the mouth to make a sound, it is reasonable to suppose that air can also be inspired through the mouth.

Perhaps the most complete evidence with regard to the possibility of the elephant's breathing through the mouth is that supplied in a personal communication from Dr. Ludwig Zukowsky of the Hagenbeck Zoological Park at Altona-Stellingen, near Hamburg. We are indebted to Dr. Zukowsky for his extremely careful and convincing discussion of this point. Both Dr. Zukowsky and particularly Captain Johansen, who has during forty-five years transported to the Hagenbecks over eight hundred elephants, are of the conviction that the elephant, like all other mammals and also man, *can* breathe through either the mouth or the trunk, as necessity arises, but uses the trunk relatively more than the mouth. In their collection of animals they have now (1935) a half-grown elephant that has a hypertrophied molar. Consequently its mouth is practically always open. Zukowsky observed this animal in deep sleep and noticed that the mouth was always open and warm air could be felt issuing from it. This observation continued for ten minutes or more and was confirmed by an attendant. It was concluded that the elephant during this time breathed mainly, if not exclusively, through the mouth and, indeed, snored. Zukowsky also has noticed that when his elephants are marching about for exhibition purposes, one behind the other and each holding onto the tail of the one in front with its trunk, this particular animal presses its trunk so strongly against the tail of the elephant in front that respiration through the nose appears to be extremely difficult. Recently Zukowsky walked very close to this animal and was convinced that there was a strong respiration through the mouth.

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[1] Watson, M., Journ. Anat. and Physiol., 1874, **8** (2d ser., 7), p. 90.

[2] Weber, M., *Die Säugetiere, Einführung in die Anatomie und Systematik der recenten und fossilen Mammalia,* Jena, 1927, 2d ed., **I** (Anatom. Teil), p. 303.

Professor T. Wingate Todd, of the Western Reserve University, Cleveland, Ohio, who has apparently made more autopsies of elephants than any other man, has given the Nutrition Laboratory a statement regarding the mouth breathing of the elephant, from which we are permitted to quote as follows:

> "That the animal can fill his trunk with water and then walk a considerable distance before ejecting it shows that under certain circumstances he can breathe through his mouth. But I am equally certain that there are other circumstances, as when he is lying on his side and sick, when he can not. That he should breathe through his mouth except in certain special circumstances I can not believe, and I do not know whether those circumstances would include a bag at the free end of the trunk, for my own experience, as I have already mentioned, is against it. But that he does breathe through his mouth when there is water up his trunk I think is certain."

It thus appears definitely established that, although the elephant for the greater part of the time breathes exclusively through its trunk, it is possible for it, when necessary, to breathe through the mouth. Furthermore, as will be demonstrated clearly later (see page 267), the metabolism of the elephant Jap as represented by measurements of the respiratory exchange through the trunk alone was 29 per cent lower than the metabolism as represented by measurements in the respiration chamber of the respiratory exchange of the entire body. This we consider indisputable evidence that considerable respiration takes place through the mouth of the elephant. Hence, from the standpoint of gaseous exchange measurements, any type of breathing appliance that does not cover the elephant's mouth as well as the trunk must be considered physiologically faulty, because of the possibility of some inhalation and exhalation of air through the mouth. Nevertheless, in view of the special type of data that can be secured with the elephant by application of a trunk-breathing appliance, a series of trunk respiration experiments were included in this study. As a respiration chamber was constructed especially for measurements of the total gaseous metabolism, the trunk-breathing experiments were designed primarily for securing observations that could not otherwise be obtained. A trunk-breathing appliance furnishes an isolated channel for the loss of respiratory gases from the lungs, excluding any loss of gases from the rest of the body. With it one can study the composition of the air as discharged directly from the lungs (not diluted with chamber air), the rate of respiration, and the depth of respiration. These observations of themselves are of value even if the respiratory exchange measurements thus obtained can not be used as indices of the total metabolism.

BRODY'S TRUNK-BREATHING EXPERIMENTS

In his comprehensive study on the growth and development of domestic animals, Brody and his associates, at the University of Missouri, made some metabolism tests on elephants, the results of which have been very briefly reported.[1] His apparatus has already been described on page 57 of this monograph. We wish to express our appreciation to Professor Brody for his extreme courtesy and generosity in placing all his original protocols (including spirometer tracings) in our hands, with permission to publish whatever wished of his data. His measurements of the respiration rate and the volume of respiration have been discussed on pages 114 and 121.

On August 30, 1932, a female elephant (No. 1), 40 years old, with a reputed weight of 3630 kg., was studied in the forenoon and again in the afternoon. From two 6-minute periods of measurement at 11 a.m. Brody calculated the *total* 24-hour heat production to be 23,270 calories and 24,883 calories. The same elephant, at 5 p.m. on the same day, measured in a 10-minute period, was found to have a calculated heat production of 43,238 calories. During these three measurements the animal was standing. On this same day a male elephant, 10 years old, weighing approximately 1360 kg., was studied in a 12-minute period at 5 p.m., while standing, and from the data secured the heat production has been calculated to be 22,886 calories per day. A year later, on August 4, 1933, a female elephant (No. 52), 40 years of age, with a reputed weight of 4127 kg., measured in a 6-minute period at 5.30 p.m., had a calculated heat production of 52,128 calories. At this time the animal was standing. At 6 p.m., when the animal was lying, a 6-minute period of measurement showed a heat production of 44,760 calories. On August 4, 1933, another female (No. 51), 35 years of age, with a reputed weight of 3743 kg., in a 4-minute and a 3-minute period of measurement at about 5.30 p.m., while standing, was found to have a heat production of 55,224 and 52,032 calories, respectively.

The following corrections in Brody's statements regarding these experiments are, unfortunately, necessary. In table 1 in his published report, in which his general results are given in abstract, the first line represents "Elephant, 1 male & 1 female." This should read "three females." Furthermore, as indicated in a later publication by Brody,[2] there is a typographical error in the value recorded for the average basal metabolism of these three females, and the average heat production per day of elephants with an average weight of 3800 kg. should not have been given in his table 1 as 20,924 calories but as 30,924 calories. According to a letter from

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[1] Brody, S., Procter, R. C., and U. S. Ashworth, Univ. Missouri, Agric. Expt. Sta., Research Bull. 220, 1934.

[2] Brody, S., and R. C. Procter, Univ. Missouri, Agric. Expt. Sta., Research Bull. 222, 1935, Errata under Foreword.

Brody, he accepted the highest heat value for elephant No. 52 of 52,128 calories, the highest value for elephant No. 51 of 55,224 calories, and the two lower, well-agreeing values for elephant No. 1, averaging about 24,000 calories. From these four results, Brody derived an average value and then, in an attempt to correct them to the basal metabolism level, he deducted 30 per cent for the influence of standing and the influence of food. His final figure, therefore, was 30,924 calories and not 20,924 calories. The three elephants each weighed approximately 3800 kg., averaging 3833 kg., according to the assumed weights as reported by the trainers.

The heat production of elephant No. 1 was, in the first two periods of measurement, about 24,000 calories or only half as great as that of Nos. 51 and 52. In the third period it was much nearer a level of 50,000 calories. On the supposition that the basal metabolism measurement is often high rather than low and that two well-agreeing periods may be taken as indicating the probable basal metabolism, Brody accepted the two lower values. Several facts militate against this use. In the first place, no special note was made that the elephant was extremely vigorous or unruly in the third period. It is hardly conceivable that the metabolism of 43,238 calories could have been determined exclusively by an internal factor, and yet no other factor except muscular work could increase the metabolism as much as 100 per cent. Secondly, the higher value is a reasonably close approximation to the values found by Brody on Nos. 51 and 52, which weighed essentially the same as No. 1. In the third place, as stated on page 88, elephant No. 1 studied by Brody was the same animal that we studied, namely, Jap. Anticipating later discussion of our own measurements (see page 247), we would point out that our trunk-breathing experiments with this elephant showed a heat production averaging 46,600 calories. On the assumption that the nutritive state of Jap at the time of our observations was not significantly different from that at the time of Brody's measurements, it is justifiable to consider that the average value of 46,600 calories supports Brody's one value of 43,238 calories. For all these reasons it is believed that Brody's two measurements on Jap indicating a heat production of 24,000 calories are too low and strongly suggest the existence of a systematic error of some sort in the technique. The conclusion is that Brody, in deriving his average value for the three elephants, should have used the value of 43,238 calories for Jap, which, together with the values of 55,224 and 52,128 calories for the other two animals, would result in an average, uncorrected for the effects of standing and food, of 50,200 calories. Applying Brody's correction of 30 per cent, the reduced value is 35,140 calories instead of Brody's average of 30,924 calories.

It so happens that this erroneous average value of 20,924 calories occurs only in table 1 in Brody's report. In his chart (fig. 1) the value is correctly plotted as 30,924 calories. If for Jap the higher heat production of 43,238 calories is accepted as the more probable, since it is more nearly in accord with the heat production of the other two elephants of the same weight and with our own subsequent measurements on this same animal, the plotted point for elephants on Brody's chart would lie measurably higher than as shown in his published report. This is not the place to discuss in detail the possible errors in the trunk-breathing method of measuring the metabolism. These errors will be treated later (page 247), when our own results by a somewhat different method are presented. The important feature of Brody's experiments is that they represent the first attempt to secure an approximate figure for the basal metabolism of the elephant. It is extremely unfortunate that in his table, which will be referred to far more frequently than will his chart, there is an error in the heat value recorded for the 3800-kg. elephant of at least 10,000 calories or, as recomputation of the data would suggest, more nearly 15,000 calories.

TRUNK-BREATHING EXPERIMENTS ON THE ELEPHANT JAP

Procedure of Experiments

It was hoped at the start of these experiments that measurements of trunk breathing might be made with Jap both when standing and when lying. In spite of the extreme docility of the animal, however, it required one whole day (March 16) to train her to put her trunk into the tube arrangement illustrated in Plate 7 (page 58) and allow it to be held there, tightly sealed, for eight or nine minutes. Hence measurements only in the standing position were attempted, and on March 17 three successful periods of measurement with the trunk-breathing appliance (open-circuit principle) were secured, each from 7 to 9 minutes long. The procedure in carrying out these measurements was as follows.

The elephant was placed in the respiration chamber with the head toward the open door and was trained to put her trunk through the opening A (Plate 2B, page 30) in the side of the chamber and into the breathing appliance, L. During the first day, March 16, the cap (n, Plate 7) was not placed on the end of the tube L and, as Jap's trunk came reaching through the tube, lumps of sugar were fed to her. Hence she was willing to keep the trunk in the tube for an indefinite period, searching for food. It perhaps was a mistake that she could not see just what was happening. Subsequent experience with elephants leads to the belief that it would have been far better for her to have seen all that was going on. On the second day after Jap had become accustomed to the breathing appliance, the trunk, upon being inserted in the tube, was tightly bound to the tube, first by a length cut from an automobile inner tubing, and then by a pure gum rubber bandage about 5 cm. wide and 90 cm. long. A strip of adhesive tape was then wound around both the inner tubing and the rubber bandage, to hold them in place. Under these conditions the closure was tight. To insure permanency of contact, the trainer, Dumont, assisted by R. C. Lee of the Nutrition Laboratory, held Jap's head and trunk closely against this closure, and to aid in persuading the animal to retain this position for several minutes, another trainer standing nearby put lumps of sugar into her mouth from time to time. Whether or not this feeding of sugar contributed to any considerable amount of mouth breathing is unknown. The elephant's mouth is usually moving more or less, even when the animal is not eating. Although the sugar may have been a factor contributing to mouth breathing, there would have been no assurance, if the animal had not been fed, that air would not have escaped through the mouth unless the mouth itself had been firmly closed and held closed. This latter procedure seemed, even with this most cooperative and intelligent animal, an absolute impossibility.

When the closure between the trunk and the tube L had been well bandaged, the cap at the end of the tube was rapidly put in place, and a strip of adhesive tape, t, was wound around this particular closure.

Before the trunk was inserted in the breathing appliance, one of the blowers in the blower box (Plate 5, page 40) had been set in operation, with its butterfly valve so adjusted that the blowers were ineffective in drawing air through the system. After the closures had been made at both ends of the tube L, the blower was adjusted to draw air through the system at such a rate as to keep the excursions of the spirometer bell about midway of the height of the spirometer. (See page 60.) As soon as equilibrium was established, which occurred when the elephant had been breathing about thirty seconds through the system, the meter M (fig. 5, page 59) was read, the temperatures on the thermometers T_1, T_2, and T_3 were read, and the level of the spirometer bell was simultaneously noted. The experiment then continued as long as the elephant's trunk could be held in place without too great effort on the part of the attendants. During the experiment one of the assistants counted the number of upward movements of the spirometer bell, which served as an index of the expiratory phase of respiration. After the seal to the trunk was broken, the blower was stopped as soon as the spirometer bell was at essentially the same position as at the start of the experiment, the meter was again read, and the temperatures were noted. After the seal was broken, the trunk was withdrawn from the tube, the rubber bandages and inner tube which remained on the elephant's trunk were removed, and the elephant was freed. Samples of the expired air were collected during the experiment for subsequent analysis, as explained on page 60.

The temperature of the barn during the three periods of measurement on March 17 was 16°, 17°, and 18° C., respectively. The environmental temperature for twenty-four hours prior to the tests had ranged from 9° to 23° C. The duration of the periods was 7, 9, and 8 minutes, respectively.

Analysis of Results

In the calculation of the results of these trunk-breathing experiments the difference between the meter readings at the start and the end of each period of measurement was corrected for the meter factor, converted from cubic feet to liters, and reduced to standard conditions of temperature and pressure by the use of standard tables for this purpose.[1] The reduced meter reading was then multiplied by the percentage of oxygen deficit in the expired air (corrected for methane in air sample) as determined by gas analysis, and this result was divided by the length of the period to obtain the oxygen consumption per minute. The methane production was calculated from the reduced meter reading and the percentage of methane in expired air. Division of the percentage of oxygen deficit by the percentage of carbon-dioxide increment (corrected for the percentage of carbon dioxide in outdoor air) gave the *apparent* respiratory quotient. The heat production was calculated from the oxygen consumption at the caloric value indicated by a respiratory quotient of 1.00, *i.e.*, 5.047 calories per liter of oxygen. The results of the several calculations are tabulated in table 39.

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[1] Carpenter, T. M., Carnegie Inst. Wash. Pub. No. 303A, 1924, tables 7 and 8, pp. 39 and 55.

Apparent Respiratory Quotient in Trunk-Breathing Experiments

In the orientation experiment on March 16 there was one period of measurement lasting 7 minutes. Unfortunately no record was secured of the ventilation rate, but samples of the air leaving the spirometer and passing through the meter were obtained and subjected to gas analysis. According to these analyses the carbon-dioxide increment in the air expired by the elephant was 3.83 per cent, the oxygen deficit was 3.54 per cent, and the apparent respiratory quotient was 1.08. These values are, in general, somewhat higher than the corresponding values recorded in table 39 for March 17. The apparent respiratory quotients obtained with Jap in these trunk-breathing experiments indicate the combustion chiefly of carbohydrates. That these quotients of over 1.00 were coincidental with the feeding of relatively large amounts of cane sugar probably does not indicate the immediate oxidation of sugar, although the sugar may have contributed to the relatively high quotients.

Table 39—*Trunk-breathing experiments with elephant Jap (March 17, 1935)*

Ventilation rate per minute[1]	CO_2 increment[2]	O_2 deficit[3]	Apparent R.Q.	Methane		Total heat production per 24 hours
				Per cent	Total per 24 hours	
liters	*p. ct.*	*p. ct.*			*liters*	*cal.*
209	2.98	2.78	1.07	....	109.0	42,153
209	3.29	3.11	1.06	0.035	108.8	47,167
232	3.33	3.00	1.11	.036	119.5	50,511

[1] Reduced to 0° C. (dry) and 760 mm.
[2] Corrected for CO_2 in outdoor air.
[3] Corrected for methane in sample.

Another factor that plays a rôle in the consideration of these apparent respiratory quotients is that Jap, although extraordinarily docile and gentle, was nevertheless agitated somewhat by the experiment. It was an experience she had undergone, to be sure, about three years previously with Brody. Yet there is every reason to believe that as a result of the agitation there was probably a certain amount of *over*-ventilation or "Auspumpung," a phenomenon common enough in respiration experiments with humans. Hence the apparently excessive production of carbon dioxide and the seeming conversion of carbohydrate into fat may be explained by a relatively slight over-ventilation of the lungs due to the novel experience.

In these trunk-breathing experiments no attempt has been made to calculate the non-protein respiratory quotient, much less the effect upon the quotient of the carbon dioxide accompanying the production of methane.

The carbon dioxide produced by fermentation may be discharged directly from the anus, directly from the mouth by eructation, or through diffusion from the lungs. In this latter case the amount discharged depends upon the solubility, transport, and diffusion of carbon dioxide and methane in the body fluids. It is hardly to be expected that the solubility and diffusion will be such that the ratio of methane to carbon dioxide discharged by the lungs will be as 1 is to 2.6, as has been found in experiments in which measurements of methane and carbon dioxide from fermentation *in vitro* have been made.[1] The proportion of carbon dioxide with reference to the methane might be a little more or a little less. Both these factors will be discussed in extenso in treating the apparent respiratory quotients as found in the respiration chamber experiments. (See page 261.)

Methane in Expired Air

The significant feature in the trunk-breathing experiments was that methane was found to be present in the air expired from the trunk of the elephant. On March 16 two analyses were made of samples of air expired through Jap's trunk. Both air samples were withdrawn from the pipe between the blower box and the meter (see page 60), one being collected in a sampling pump and the other in the Fox bag. These analyses showed that the expired air had a methane content of 0.026 and 0.042 per cent, respectively.[2] On March 17 two analyses of samples collected in the Fox bag showed 0.035 and 0.036 per cent. These percentages correspond to about 1 per cent of the percentages noted for carbon-dioxide increment in the expired air. The calculated volume of methane eliminated by Jap in the expired air ranged from 109 to 120 liters per 24 hours and averaged 112 liters.

To supplement the observations made upon Jap, the composition of the expired air of elephant No. 4 was studied on September 27 and on October 7, 1935, at Benson's animal farm in New Hampshire. A sampling pump holding about 400 cc. was fitted with a 15-cm. rubber tube. This tube was inserted into one of the openings in the elephant's trunk. During the first expiratory blast, expired air was drawn into the pump and then rejected. During the second expiratory blast the pump handle was drawn out to its full capacity, and the sample of expired air thus obtained was analyzed for carbon-dioxide and methane content. The results obtained were as follows:

	CO_2 increment	Methane
	p. ct.	*p. ct.*
Sept. 27........	4.618 1.966 1.887	0.038 .021 .024
Oct. 7..........	6.050 5.661 5.236	.035 .029 .035

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[1] Krogh, A., and H. O. Schmit-Jensen, Biochem. Journ., 1920, 14, p. 686.

[2] Brody did not measure the methane production in his elephant experiments.

On the first day, owing to inexperience in technique, it was found difficult to draw a sample of expired air into the ordinary sampling pump at the proper moment during expiration so as to obtain the maximum percentage of carbon dioxide in expired air. Two of the three analyses on this date show reasonably close agreement, and all three indicate that the percentage of methane in expired air corresponds to about 1 per cent of the percentage of carbon-dioxide increment. On October 7 samples of expired air were obtained at the end of maximum expirations that more nearly approximated alveolar air. On this date the carbon-dioxide increment was as high as 6.05 per cent. The methane percentages ranged from 0.029 to 0.035 and were from one-half to three-fourths of one per cent of the carbon-dioxide increment. The difference between the relationships of methane and carbon dioxide on October 7 and on September 27 may be accounted for by the difference in the state of feeding. No attention was given to the quantity and quality of the food prior to these tests.

Although the presence of methane in the air from the trunk was thoroughly established in the case of these two animals, Jap and No. 4, the importance of this observation as contributing evidence regarding the solubility of gases in the blood and their subsequent discharge into the lungs was such that in November 1935 two other samples of expired air were taken from elephants No. 15 and No. 47 in Florida. Analyses of these samples in Boston showed that the expired air of No. 15 contained 3.090 per cent carbon dioxide and 0.035 per cent methane, and that of No. 47 contained 2.106 per cent carbon dioxide and 0.021 per cent methane.

The presence of methane in the expired air shows that there is a transport of fermentation gases from the alimentary tract into the blood and into the lungs, from which the methane is diffused into the air leaving the lungs. It is possible for some animals to discharge some methane through the nose or mouth by eructation (see page 256), but from the anatomical structure of the elephant and the location of its trunk it is hardly conceivable that the methane found in the air expired through the trunk was other than that actually diffused into the blood stream and then given up to the air in the lungs. The percentage of methane in expired air would normally be affected by the total ventilation of the lungs, precisely as is the percentage of carbon dioxide. Although determinations of methane in expired air were not made with all the elephants, the results obtained with four show that methane is a constant constituent of the air exhaled through the trunk and that, on the average, *the methane content of the air expired through the trunk of the elephant is essentially one per cent of the carbon-dioxide content.* Thus, when the carbon-dioxide content is about 3.3 per cent, the methane content is 0.035 per cent. This amount of methane is sufficient to prove the presence of this fermentation gas in the expired air, uncontaminated by any fermentation gas from the rectum.

The presence of methane in the expired air of the herbivore has been previously noted in some instances. It is possible to prove its presence only in experiments in which a mask or a tracheal cannula is employed. With the steer, the cow, and the sheep such observations have not been made, but with the horse and the goat they have been made. Discussion of fermentation gases and particularly methane in expired air is given by Magee and Orr [1] in reporting their experiments on the goat. Employing the mask, they found the percentages of methane and carbon dioxide in expired air, but unfortunately do not report these in their several publications, giving only the derived calculations for respiratory quotient and heat production. Zuntz and Lehmann,[2] using a tracheal cannula, found as a result of a number of experiments with a horse that the expired air contained, on the average, 0.038 per cent methane and 3.023 per cent carbon dioxide. The individual observations, however, show that there was an enormous variability in the percentages of methane, from 0.000 to 0.106 per cent, without a comparable change in the amount of carbon dioxide accompanying this gas. Their experiments as a whole would suggest strongly the possibility of eructation by the horse. On the other hand, the remarkable uniformity in the relationship between the percentages of carbon dioxide and methane in the expired air of the elephant lead to the conclusion that there is a resorption of these gases from the intestinal tract and a subsequent transport to the lungs rather than any intermittent eructation.[3]

The technique of determining the methane in air samples was by no means satisfactory at the time of Zuntz and Lehmann. Consequently one should not criticize their results too adversely. Furthermore, the fact that Zuntz and Lehmann report that there was hydrogen in a number of the air samples (an element the presence of which in intestinal fermentation is very much debated at the present time) accentuates again the difficulties at that time of the determination of small amounts of these gases. The use of the Carpenter gas-analysis technique, which has been thoroughly tested with definite and minute amounts of methane, is, however, without criticism and gives a true picture of the composition of the air expired from the trunk of the elephant. The chief difficulty was in securing samples. The restlessness of the elephant, the contamination of the sample with outdoor air, and the inability to secure a large enough sample to be representative were all factors contributing toward uncertainty in the results. However, in only one of our series of analyses (the second series with No. 4) was any significant deviation noted from the general picture—that one volume of methane accompanies every one hundred volumes of carbon dioxide in the air expired from the trunk.

In the classic work of Zuntz and Hagemann [4] on the metabolism of the horse no determinations were made of methane in the expired air, although a tracheal cannula was used. The authors compute the methane from the usual formula, in which it is assumed that for each one hundred grams of crude fiber digested 4.7 liters of methane are produced. Thus Zuntz himself seems to have had doubt with regard to the accuracy and significance of the earlier work carried out by himself and Lehmann, in which such

[1] Orr, J. B., and H. E. Magee, Journ. Agric. Sci., 1923, **13**, p. 456.

[2] Zuntz, N., and C. Lehmann, Landw. Jahrb., 1889, **18**, pp. 41 and 124 *et seq.*

[3] The method of transport of methane through the blood has been discussed by Zuntz and Lehmann, but the evidence furnished by them is by no means conclusive, owing to the irregularity in their results.

[4] Zuntz, N., and O. Hagemann, *Untersuchungen über den Stoffwechsel des Pferdes bei Ruhe und Arbeit,* Berlin, N. F., 1898.

tremendous variations in the amount of methane in the expired air were found. Apparently, therefore, these results on the elephant are the first accurate results proving the presence of methane in the expired air other than by eructation.

So many potential errors enter into the trunk-breathing type of experimenting, when one is considering the total metabolism, that it is hardly necessary here to discuss the significance of methane as a factor in gas analysis or as a factor in the measurement of the heat production. Consideration of this point will be deferred until the chamber experiments are discussed.

Heat Production Calculated From Trunk-Breathing Experiments

Although the treatment of Jap's total heat production will be deferred until the respiration chamber experiments are considered, preliminary calculations of the heat production as indicated by the trunk-breathing experiments are reported here and will be subsequently compared with the calculations based on the chamber experiments. This comparison could have dealt solely with the measurements of the oxygen consumption, from which the heat production is calculated, but the comparison is perhaps a little clearer when the heat values are used. Hence these preliminary calculations are here introduced.

Jap's heat production, calculated from the oxygen consumption as explained on page 242, was lower in the first period than in the second and third periods. If the result for the first period is discarded, the average is 48,800 calories per 24 hours. If all three periods are used, the average becomes 46,600 calories or not far from the average for the second and third periods. Comparison of this average of 46,600 calories with the results obtained by Brody on this same animal has already been made on page 240, where it has been pointed out that one of Brody's period values agrees reasonably well with our average of 46,600 calories. If Brody's value of 43,238 calories is averaged with the three period values obtained by us, one can say that the average total heat production of Jap, *as measured by the trunk-breathing appliance,* is 45,800 calories. Owing to the uncertainty as to the justification of the assumption that the respiration of the elephant takes place entirely through the trunk, however, these values can not be accepted uncritically as representing the total heat production of Jap. The question arises, however, as to whether our feeding of sugar facilitated the escape of air through the mouth. Certainly it was not an ideal method of conducting respiration experiments. If, however, there is no connection between the esophagus and the air passages of the elephant, as has been contended, the feeding of sugar should be without any effect upon the passage of air through the trunk. Since the average of our trunk-breathing measurements on Jap is somewhat higher than the one accepted period value of Brody, obtained when no feeding was going on, it is probable that the feeding of the sugar did not facilitate escape of air through the mouth. Nevertheless in the final interpretation of results and particularly in comparing the trunk-breathing experiments with the studies inside the respiration chamber, it should be taken into consideration that in the trunk measurements there was great possibility for a second path for the loss of respiratory gases, which would not be measured by the spirometer and blower system.

In the open-circuit method as employed by us, if air were taken into the mouth and expelled through the nose, it would have no effect upon the measurement of the respiratory gases. Any air inhaled through the mouth would simply be the equivalent of any air entering into the trunk-breathing apparatus through the inlet valve. On the other hand, if air were expelled through the mouth at any time due to the eating of sugar, for example, the result would be to lower the measured metabolism. With the closed-circuit method as used by Brody the error may be in two directions. If the animal continually inspired a small amount of air through the mouth and exhaled it through the trunk into the spirometer, this would tend to lessen the apparent oxygen consumption. Conversely, if the animal continually expired a small amount of air out of the mouth, this would tend to increase the apparent oxygen consumption. On the basis of the trunk-breathing experiments alone, however, one could infer that Jap had a total heat production of about 45,800 calories per day. Further consideration of the accuracy of this measurement demands a discussion of the respiration chamber experiments.

Respiration Chamber Experiments

In the study of the respiratory exchange of the elephant, the trunk-breathing experiments were only an incidental feature. The special efforts to measure the metabolism of the elephant were concentrated upon the far more complicated, expensive, and time-consuming observations with Jap inside the respiration chamber. Although, as pointed out on page 238, it is perfectly possible for elephants to breathe through the mouth when occasion demands, in all probability the animal, as a general rule, does not breathe to any great extent through the mouth. Yet because of the possibility of mouth breathing there is a potential error in the metabolism measurements made with the trunk-breathing appliance. For this reason the respiration chamber experiments made almost simultaneously with the trunk-breathing experiments are of more value in indicating the probable metabolism of the elephant. With the respiration chamber, it is possible to obtain the complete measurement of the respiratory gases. It is immaterial whether air is expired through the trunk or through the mouth. Furthermore, the respiration experiments in the chamber can be prolonged for a much longer period than the 7- to 9-minute periods with the trunk-breathing apparatus. Indeed, on three days, March 11, 12, and 13, the measurements were prolonged for eight consecutive, half-hour periods.

Control test—No control was made of the accuracy of functioning of the trunk-breathing apparatus because, based upon long experience with various types of valve apparatus, there was no reason to question the mechanical functioning of the valve system employed. However, the accuracy of functioning of the respiration chamber was demonstrated by a carbon-dioxide control test, and one can have complete confidence in the results obtained by the chamber method. The technique of the carbon-dioxide control test has been explained on page 54. Such a control test was made on March 8, when from 356 to 475 liters of carbon dioxide were introduced into the chamber in each of four consecutive periods of measurement. From the results of gas analyses indicating the carbon-dioxide content of the air withdrawn from the chamber and from the metered total volumes of air passed through the chamber in these four periods, calculations were made of the volumes of carbon dioxide recovered. These calculations included the usual correction to standard conditions of temperature and pressure, the correction for any change in residual carbon dioxide in the air in the chamber during the period of measurement, and the correction for the carbon dioxide in the outdoor air entering the chamber. On the average, the volume of carbon dioxide recovered amounted to 100.2 per cent of the volume introduced.

PROCEDURE IN RESPIRATION CHAMBER EXPERIMENTS

Jap was led into the chamber and chained (with her back to the door) to two eye bolts (k, k, Plate 3A) in the floor of the chamber. Hay was placed upon the floor in front of her and was usually entirely consumed by the end of the experiment. An attendant, holding a bag containing bits of bread, sat in a chair near the corner of the chamber where the speaking tube (A, Plate 2B) was located. The electric fan inside the chamber had been started and the electric light had been lighted previous to Jap's entering the chamber. The door was then put in place, braced with the proper braces, and taped. The butterfly valve in the pipe (a, Plate 2B) conducting air into the chamber was closed, and the elephant was allowed to remain inside the chamber without ventilation until the carbon-dioxide content of the chamber air reached about 1 per cent, the optimum percentage for analysis of air by the Carpenter gas-analysis apparatus. The time required for the carbon-dioxide content to reach this level was usually about 20 minutes. The blowers and fan were started before the elephant entered the chamber so that she would become accustomed to the noise of their operation. During the preliminary period the efficiency of the blowers was rendered nil by proper turning of the butterfly valves. When the carbon dioxide had reached approximately the desired percentage, the butterfly valve in the intake pipe was opened wide and the butterfly valves on the blower box were adjusted so that the air would enter the meter at the rate which had previously been found to be essential for holding the carbon-dioxide content of the chamber air at about 1 per cent or a little lower. The adjustment of the butterfly valves could be easily made by noting the level of the float in the small rotamesser (R, fig. 2), which had been previously calibrated and found to serve as a fairly close index of the actual rate of air passing through the large meter. When the ventilation rate had been adjusted, the meter was read carefully at a given moment, a residual sample of chamber air was drawn through the petcock (E, fig. 2), and the experiment proper began. At the end of each half-hour period the Fox bags (F, F, fig. 2) were changed, samples were taken from them for analysis, a residual sample was drawn from the petcock, and the meter was read again. The thermometers recording the temperature of the air entering and leaving the meter were also read at the beginning and end of the period.

The carbon-dioxide production of Jap proved to be singularly constant from period to period, so that when the carbon-dioxide content of the air in the chamber was once raised to the proper level (*ca.* 1.0 per cent), no great change in residual carbon dioxide was to be expected. Indeed, the production of carbon dioxide and the rate of removal of the same were so constant in these experiments that the percentage of residual carbon dioxide remained essentially constant throughout an entire experiment of eight 30-minute periods.

In the experiments in which the water-vapor output was measured as well as the carbon-dioxide production and the oxygen consumption, it was necessary to increase the ventilation rate. With a ventilation rate sufficient to allow the carbon-dioxide content of the air in the chamber to be at a level of 1 per cent, not enough air passes through the chamber to bring out all the water vaporized by the animal. This is particularly true if the air entering the chamber from outdoors is saturated with water vapor, although since the air in the chamber was warmed considerably by the elephant, it obviously never was saturated at the temperature at which it left the chamber except by reason of the water vapor added to it by the elephant. A considerable increase in the ventilation rate, however, brought out all the water vapor, left no condensation inside the chamber, and yet at the same time did not lower the carbon-dioxide content of the chamber to such a point as to affect seriously the accuracy of the analyses by the Carpenter gas-analysis apparatus. With the Carpenter apparatus, although admittedly the optimum percentage of carbon dioxide in air samples is from 0.8 to 1.0 per cent, one can still obtain accurate measurements of the carbon-dioxide increment when the air sample contains only 0.4 per cent of carbon dioxide.

The attendant, Dumont, was instructed to do everything during the experiment that would contribute toward minimum physical exercise on the part of the animal. To accomplish this, he found it most advantageous to throw pieces of bread, a half slice at a time, onto the hay in front of Jap, from where he sat near the left, hind leg. In Jap's search for the bread in the hay, trunk movements were necessary, but on the whole the body movements were very few. The bread and the hay served the purpose of keeping Jap contented and at the same time reasonably quiet.

At the end of the experiment a residual sample of chamber air was withdrawn for analysis, the blowers were stopped, the meter and the thermometers were read, the door was removed, and Jap was brought out and chained in her usual position in the barn.

In the first four experiments on March 10 to 13 many gas analyses were made for carbon dioxide, oxygen, and methane. In these experiments the percentages of methane and the "apparent respiratory quotients" calculated from the carbon-dioxide increment and the oxygen deficit remained so nearly the same that in the later experiments on March 14 and March 15 the assumption was made that the respiratory quotient would be the same as on the average for the preceding days and the gas analyses were confined to determinations of the carbon-dioxide increment only for each individual period and the determination of methane in only one period, and no analyses were made of the oxygen deficit. This materially lessened the number of analyses necessary for these tests.

TABLE 40—*Typical calculation of oxygen consumption during a respiration chamber experiment (March 13, 1935—Period 1)*

Meter readings

End	2,585,703	cubic feet
Start	2,583,952	" "
Difference	1,751	" "
Times meter factor	×1.01	
Corrected meter reading	1,769	" " × 28.32[1]=50,098 liters

Barometer and temperature readings

Barometer	745 mm.
Tension aq. vapor[2]	12 "
Corr. barometer	733 "

	Dry bulb Start	Dry bulb End	Wet bulb Start	Wet bulb End
Air entering meter	19.8°C.	20.4°C.	....	....
Air leaving meter	21.0°C.	19.3°C.	16.8°C.	16.5°C.
Chamber, at top	19.0°C.	19.1°C.		

Data by gas analysis

Residual CO_2 (p. ct.)[3]	Start	End
	0.782	0.736
	.787	.....
Avg.	.785	.736

Aliquot sample (p. ct.)	
CO_2 increment	0.713[4]
O_2 deficit	.726[5]
Apparent R. Q.	.982

Change in residual CO_2 in chamber

	Start	End
Volume of chamber[6]	39,117 l.	39,117 l.
Times factor for reduction to 0°C. (dry), 760 mm.	×0.899[7]	×0.897[7]
Corrected volume of chamber	35,166 l.	35,088 l.
Times per cent residual CO_2	×.00785	×.00736
Liters residual CO_2	276.1 l.	258.2 l.
Change in residual CO_2	—17.9 l.	

Oxygen consumption

Corrected meter difference	50,098 liters
Times factor for reduction to 0°C. (dry), 760 mm.	×0.898[8]
Reduced meter reading	44,988 liters
Times per cent oxygen deficit in aliquot sample	×.00726
Apparent O_2 consumed	326.6 liters
Less O_2 represented by change in CO_2 residual	—18.2[9] "
Total O_2 consumed per 30 minutes	308.4 "

[1] Liters per cubic foot.

[2] Based on average dry and wet bulb temperatures of air leaving meter. See table 2, p. 15, in Carpenter's tables (Carnegie Inst. Wash. Pub. No. 303A, 1924).

[3] Not corrected for CO_2 in outdoor air.

[4] Corrected for CO_2 in outdoor air.

[5] Corrected for methane in the aliquot sample, which was assumed to be the average of the methane percentages determined in periods 2, 5, and 7 on March 13.

[6] Corrected for volume of elephant and trainer; no correction for volume of chair and hay.

[7] Obtained by using the dry bulb temperature of air entering meter at start and end of period, respectively, and corrected barometric pressure of 733 mm. (See tables 5 and 6, pp. 32 and 34, of Carpenter's tables.)

[8] Based on average (20.1°C.) of all four dry bulb temperatures of air entering and leaving meter and corrected pressure of 733 mm. (See tables 5 and 6 of Carpenter's tables.)

[9] Change in CO_2 residual (−17.9 l.) divided by apparent respiratory quotient (0.982).

TYPICAL CALCULATION OF A RESPIRATION CHAMBER EXPERIMENT

A typical calculation of the oxygen consumption during one of the half-hour periods of measurement with the respiration chamber is illustrated in table 40. The carbon-dioxide production was calculated in the same manner by applying the percentage of carbon dioxide found in the aliquot sample to the reduced meter reading and correcting for change in residual carbon dioxide. The methane production was obtained as explained on page 242. The apparent respiratory quotient was calculated by dividing the carbon-dioxide increment (corrected for carbon dioxide in outdoor air) by the oxygen deficit (corrected for methane in the air sample). Obviously in these calculations the products of respiratory exchange ascribable to the presence of the keeper inside the chamber have not been taken into account. Correction for the metabolism of the man will be deferred until consideration is given to the heat production.

ANALYSIS OF MEASUREMENTS OF THE PRODUCTS OF RESPIRATION

The experiments with Jap inside the respiration chamber covered a period of six days, from March 10 to March 15, inclusive. The details of the results are recorded in table 41. All periods of measurement were 30 minutes long. The environmental temperature inside the respiration chamber was regulated by the heat production of the elephant, a constant factor, and on the average varied from only 20.0° to 24.7° C. The environmental temperature prior to the experiments, that is, the barn temperature, was difficult to control, although an attempt was made to do so by opening and closing the barn doors and heating with an inadequate stove. In two instances, March 14 and 15, the barn temperature before the experiment was as low as 0° C. (32° F.). These barn temperatures (recorded in the first column in table 41) illustrate the great extremes in temperature to which Jap was subjected, a procedure wholly contrary to the usual physical care and protection given to these valuable animals.

The ventilation rate per minute on the first two days was approximately 1000 liters, and the regularity in the rate from period to period showed the perfect functioning of the blowers. On the remaining days of the experimental series the ventilation rate was increased from 50 to 70 per cent, to prevent condensation of water inside the chamber. On these days also the rate was extraordinarily constant from period to period. The optimum percentage of carbon dioxide for the Carpenter gas-analysis apparatus, namely, about 1 per cent, was noted in the air samples analyzed on March 10 and 11. When the ventilation rate was increased, naturally the carbon-dioxide percentage of the air was lowered.

The percentage oxygen deficit in the various periods of measurement was essentially the same as the percentage carbon-dioxide increment, and the apparent respiratory quotient was, therefore, about 1.00. Indeed, the quotients determined by gas analysis on the first four days remained so close to 1.00 that it was deemed justifiable to omit the time-consuming oxygen determinations in the last three experiments, for the oxygen consumption on these days could be calculated with reasonable correctness from the accurately measured carbon-dioxide production and the average of the previously determined apparent respiratory quotients. The time thus saved was devoted to a study of the water-vapor output.

The percentage oxygen deficit in the chamber air samples and the oxygen consumption per minute are recorded in table 41 for those periods when these measurements were actually made. Carbon-dioxide values are available for all periods, as direct determinations of this factor were made in all cases. Since the apparent respiratory quotients were at a level of about 1.00 throughout the series, the carbon-dioxide measurements may be taken as an index of the variability in metabolism from period to period. On the whole, there was reasonable uniformity in the carbon-dioxide production per minute on any given day. The most striking deviation occurred on March 10, when the range was from 7.77 to 10.13 liters per minute.

The determinations of the oxygen deficit in the chamber air were not so frequent as those of the carbon-dioxide increment, but from the uniformity in the apparent respiratory quotients it is clear that the carbon-dioxide values alone give a good indication of the relative metabolism from period to period. The twelve determinations of the oxygen consumption, expressed in the last column of table 41 as liters per minute, vary from a minimum of 7.64 liters on March 10 to a maximum of 10.28 liters on March 13. It possibly was an error that the oxygen consumption was not determined more frequently, but the uniformity in the apparent respiratory quotients led us to forego the continuous oxygen measurements and, as stated above, to concentrate during the last two days of the experimental series upon a study of the water-vapor output.

With the elephant and even more strikingly so with ruminants, the production of methane is a perplexing factor. This was measured frequently enough in the experiments with Jap to establish its presence. Strictly speaking, the volume of methane produced should be considered in any discussion of the respiratory quotient. But since there is an accompanying production of carbon dioxide during fermentation, it is obvious that for an intelligent interpretation of the influence of the fermentation processes as a whole one should know not only the amount of methane produced but the amount of carbon dioxide produced by such fermentation. The first attempt to analyze this influence of the fermentative process will be a consideration of the methane production. Since the chief importance of the respiratory quotient and the attempt to evaluate or correct for the influence of methane in metabolism is in association with the heat calculations, discussion of the respiratory quotient will be left until the methods of computing the heat production are treated in the succeeding pages.

METHANE PRODUCTION

Methane was determined in eleven different samples of chamber air during the six days of measurement. It was an experimental error that it was not determined oftener, but in order to study the water-vapor output, the methane analyses had to be foregone on the last two days (except in one period). The picture as a whole shows that *the chamber air contained not far from 0.033 per cent methane, corresponding to approximately 3 or 4 per cent of the carbon-dioxide increment.* In the calculation of the heat pro-

TABLE 41—*Gaseous exchange measurements on the elephant Jap in respiration chamber experiments*

Date, previous environmental temperature,[1] and average exper. temperature	Period No.[2]	Ventilation rate per minute[3]	CO_2 increment[4]	O_2 deficit[4]	Apparent R.Q.	Methane		Per minute	
						Per cent	Total per 24 hrs.[5]	CO_2 eliminated	O_2 consumed
1935		*liters*	*p. ct.*	*p. ct.*			*liters*	*liters*	*liters*
Mar. 10 (p.m.)	1	1003	0.934	0.917	1.02	....	....	10.13	9.94
10° to 15°C.	2	1013	.945	....	....	0.033	....	9.41	....
20.2°C.	3	1037	.925	....	....	.036	....	9.25	....
Blanket worn	4	1038	.875	.861	1.02	....	....	7.77	7.64
Average	....	1023	....	....	....	....	501	9.14	....
Mar. 11	1	1018	.896	.883	1.01	....	....	10.42	10.26
9° to 14°C.	2	1038	.956	....	....	.026	....	9.88	....
20.0°C.	3	1033	.935	....	....	.029	....	9.06	....
	4	1041	.896	.906	.99	....	....	9.01	9.11
	5	1054	.844	.852	.99	....	....	8.73	8.81
	6	1046	.849	....	....	....	....	8.74	....
	7	1060	.856	....	....	.045	....	9.16	....
	8	1049	.863	.859	1.00	....	....	9.14	9.10
Average	....	1042	....	....	....	....	510	9.27	....
Mar. 12	1	1463	.763	.805	.95	....	....	9.31	9.83
10° to 22°C.	2	1481	.690	....	....	.030	....	9.75	....
23.0°C.	3	1482	.658	....	....	....	....	9.24	....
	4	1478	.634	.635	1.00	....	....	9.36	9.37
	5	1497	.650	....	....	....	....	9.78	....
	6	1503	.637	....	....	....	....	9.62	....
	7	1486	.649	....	....	.032	....	9.63	....
	8	1459	.650	.628	1.04	....	....	9.62	9.30
Average	....	1481	....	....	....	....	661	9.54	....

Mar. 13 3° to 22° C. 23.1° C.	1	1500	.713	.726	.98	...	...	10.10	10.28
	2	1496	.710	...	...	.026	...	10.64	...
	3	1475	.710	...	...	...	...	10.04	...
	4	1485	.627	.621	1.01	...	...	8.54	8.46
	5	1486	.605	...	...	.026	...	8.90	...
	6	1489	.594	...	...	...	...	8.62	...
	7	1500	.584	...	...	.031	...	8.81	...
	8	1490	.582	.549	1.06	...	...	8.68	8.18
Average	...	1490	...	...	...	...	665	9.29	...
Mar. 14 (a.m.) −1° to 20° C. 21.5° C.	1	1729	.635	...	...	...	...	10.14	...
	2	1690	.602	...	...	...	...	10.00	...
	3	1692	.587	...	...	...	...	9.51	...
	4	1682	.548	...	...	...	...	8.78	...
Average	...	1698	...	...	...	...	758	9.61	...
Mar. 14 (p.m.) 15° to 20° C. 23.5° C.	1	1664	.637	...	...	...	...	10.63	...
	2	1673	.646	...	...	...	...	10.77	...
	3	1675	.642	...	...	...	...	10.37	...
Average	...	1671	...	...	...	...	746	10.59	...
Mar. 15 0° to 23° C. 24.7° C.	1	1646	.625	...	...	...	...	9.33	...
	2	1653	.592	...	...	.042	...	9.68	...
	3	1659	.588	...	...	...	...	9.62	...
	4	1665	.600	...	...	...	...	10.09	...
	5	1689	.588	...	...	...	...	9.49	...
Average	...	1662	...	...	...	...	742	9.64	...

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[1] Barn temperature for 20 hours preceding experiment.

[2] Consecutive 30-minute periods.

[3] Reduced to 0° C. (dry) and 760 mm.

[4] Results of analyses of aliquot samples of chamber air. CO_2 increment has been corrected for CO_2 in outdoor air.

[5] Values for March 10 and 11 based on average per cent methane noted on those dates; values for March 12 to 15 based on average per cent methane noted on those dates.

duction from the measurements of the respiratory exchange, the total methane production plays a considerable rôle. For this reason the methane production per 24 hours has been calculated for the different experimental days. On the first two days when the ventilation rate was about 1000 liters per minute, the average methane content of the chamber air samples was 0.034 per cent. The average ventilation rates per minute on March 10 and 11 have been multiplied by 0.034 per cent to obtain the average methane production per minute on these dates, and the per minute values have been converted to the 24-hour basis. On the remaining days from March 12 to 15, inclusive, when the ventilation rate was nearer 1500 liters per minute, the average ventilation rates have been multiplied by the average of the percentages of methane noted on March 12, 13, and 15, namely, 0.031. The 24-hour methane production ranged from 501 to 758 liters and averaged 655 liters. These values have not been corrected for any possible change in the residual methane in the chamber during the experiments, on the assumption that, because of the regularity in the period values for carbon-dioxide increment and oxygen deficit, the residual methane in the chamber would not vary greatly from period to period.

The methane measurements in the respiration chamber and in the trunk-breathing experiments indicate that there are two paths for the discharge of methane by the elephant, one in the respiratory gases exhaled through the trunk and the other through the anus. According to the trunk-breathing experiments, Jap excreted through the trunk approximately 112 liters of methane per 24 hours, and according to the respiration chamber measurements about 655 liters from the lungs and the anus. As will be subsequently shown (see page 267), the gaseous metabolism as measured by means of the trunk-breathing appliance is 29 per cent less than that measured by means of the respiration chamber. There is every reason to believe that this difference is ascribable to the fact that the measurement of the ventilation of the lungs did not include the gaseous exchange through the mouth. Hence the 112 liters of methane excreted through the trunk should be increased in the ratio of 70 to 100 to approximate the true total amount of methane exhaled from the lungs. The result would be 160 liters of methane, which would be the equivalent of about one-fourth of the total methane elimination. Thus with the elephant one-fourth of the methane may be eliminated through the trunk and the mouth and three-fourths through the anus.

At this point it is clear that one should consider how various animals discharge methane and other products of fermentation. With the cow and the steer the fermentation is assumed to be for the greater part in the rumen. Any gases formed there find their way rather easily up through the esophagus and out through the mouth or nose. The loss in this way may be supplemented by the absorption of these fermentation gases in the blood stream and their elimination ultimately in the lungs themselves. The passage of gas upward through the alimentary tract, through the throat and the nose, may be the result of normal diffusion and may be the result of eructation. Many writers believe this latter is the chief method for the loss of methane from ruminants. Indeed, if for any reason the esophagus is clogged with food, as for example, when cows have been overeating on clover, the free passage of this gas may not be had, the animals become bloated and may actually die, for the distance from the point of gaseous formation to the anus is so far that the gases can not well escape in this direction. On the other hand, with the horse a large amount of the gas is undoubtedly discharged through the anus. It is believed that the horse is unable to eliminate gas by means of the throat, mouth, and nose, as there is a valve which prevents it, but with the bovine this valve opens on pressure and gas escapes through the esophagus.

In the case of the horse, fermentation takes place in the cæcum and the colon. Most of the soluble carbohydrates in the food are removed before the material reaches the colon, so that the fermentation there is chiefly of crude fiber. The position of the elephant in this classification is indicated somewhat by the relative length of the intestines to the total length of the body. For example, with Carnivora the intestines are five times the length of the body, with the horse twelve times, and with the cow and the steer twenty times.[1] The length of the intestines of the horse is about 30 meters,[1] which is essentially that of the elephant's intestines.[2] Since the elephant has a much greater body length than the horse, the intestinal tract of the elephant is relatively much shorter than that of the horse. This all speaks for a shorter sojourn of food residues in the intestinal tract (see page 189) with a shorter time for fermentation and a lessened fermentative action in the case of the elephant. No indication of eructation or belching has been noted with the elephant, although this would be difficult to determine exactly. On the other hand, relatively enormous volumes of gas are given off through the anus, especially when the elephant is lying down at night. This in turn speaks for fermentation in the posterior end of the intestinal tract.

It thus appears that the situation with the elephant lies somewhat between that with the horse and the cow, for the fact that one-fourth of its methane production is eliminated through the trunk and the mouth implies that it is feasible for the elephant to lose at least a portion of the methane in this way. On the other hand, the fact that three-fourths of the methane escapes through the anus suggests an easy passage through the rear.

The demonstration of the existence of methane in the air expired from the mouth and from the trunk raises the question as to the method of its release from the body. Two possibilities suggest themselves, (1) that methane is brought up from the stomach by eructation, much as with cows, or (2) that methane is absorbed by the body fluids, carried to the lungs, and there diffused into the air which is subsequently expired. In the former case one would expect to find in analyses of several samples of expired air that the percentages of methane in relation to carbon dioxide would be very variable, depending upon whether the samples were taken at the moment of eructation or not. As a matter of fact, it has been found that in general there is a remarkably uniform relationship between the methane content and the carbon-dioxide content of expired air. This is convincing proof that, with the elephant at least, the main loss of methane is through the simple process of absorption and subsequent diffusion into the air of the lungs. The regularity in the proportion of methane to carbon dioxide in expired air could hardly be maintained, provided the methane were delivered into the nasal passage as a result of eructation, *i.e.*, intermittently, and it is hardly conceivable that all samples could be taken at precisely the moment when these eructations were taking place.

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[1] Disselhorst, R., *Grundriss der Anatomie und Physiologie der Haussäugetiere*, 6th ed., edited by E. Mangold, Berlin, 1931, pp. 230 and 234.

[2] See page 108.

Based upon these observations with the elephant it seems certain, therefore, that in respiration experiments with the horse, the cow, or the steer it would be distinctly questionable to assume that the entire methane discharged may be exclusively through the trachea in the case of the cow and steer and through the anus in the case of the horse. It is more than likely that these assumptions have been the cause of variations in the interpretations of gaseous metabolism measurements made with the tracheal cannula with these and other animals. Thus it is surprising to note that, although Orr and Magee,[1] in their discussion of the significance of methane in the calculation of the metabolism of the goat from the respiratory measurements, lay great stress upon the discharge through the trachea, they disregard completely the possibilities of any methane elimination through the anus. It is predicted that when further investigations are carried out, it will be found that there is a considerable discharge of methane through the trachea of the horse and likewise a considerable discharge from the anus of the cow and other ruminants.

Our own experience with animals has not led to any data representing *separate determinations* of the methane discharged from the trachea and the methane discharged from the anus. For many years, however, the Nutrition Laboratory has been cooperating with the Agricultural Experiment Station at Durham, New Hampshire, in respiration experiments on large domestic animals, in which many gas analyses have been made of aliquot samples of air leaving the chamber. The data are, therefore, available for comparison of the ratios between the volumes of total methane produced and the volumes of total carbon dioxide produced, as noted with these various animals. These ratios, expressed as volumes of methane for every one hundred volumes of carbon dioxide for those instances when the measurements were made with animals receiving maintenance rations and not fasting or on submaintenance rations, and also the ratio noted with Jap, are as follows: elephant, 4; horse, 4; cow, 7 to 8; sheep, 7; goat, 4.

It is thus seen that the ratio of volume of methane discharged to one hundred volumes of carbon dioxide eliminated is essentially the same with the elephant as with the horse and the goat, whereas with the cow and the sheep almost twice as much methane is eliminated with the same carbon-dioxide production.

The rôle played by methane in the experiments with the elephant is manifold. The fact that methane is produced in the elephant and may be discharged in considerable amounts in the air breathed through the trunk is important. Hence, the effect of this amount of methane upon the calculation of the respiratory exchange of the animal should be taken into consideration. The significance of methane in its relation to the carbon dioxide produced, the paths for the excretion of methane, and the influence of fermentation (the source of methane) upon the temperature of the feces, upon the digestibility, and more particularly upon the determination of the respiratory gases and the interpretation of gaseous metabolism with special reference to the heat production are all important. These factors are all closely associated with the fact that in ruminants and the elephant, among other animals, methane is produced as a product of fermentation in the intestinal tract. Under ordinary conditions no attempt is made to distinguish between the gaseous metabolism of the animal itself and the metabolism of the bacteria and infusoria of the alimentary tract. From the standpoint of the energy balance, for example, an animal must be given sufficient energy to take care not only of the demands of its own cell tissues, but likewise the demands of its parasites, as one might call them. Strictly speaking, it may be argued that to calculate the true basal metabolism of an animal one should deduct the metabolism of the bacterial and infusorial action. In any attempts to make this apportionment, methane plays a very important rôle.

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[1] Orr, J. B., and H. E. Magee, Journ. Agric. Sci., 1923, **13**, p. 457; Magee, H. E., Journ. Agric. Sci., 1924, **14**, pp. 516, 525, 600, and 619.

Rôle Played by Fermentative Action in Metabolism Studies

The methane factor enters into several phases of metabolism studies. Its effect upon the temperature of the feces (which serves as an index of the internal body temperature) and its effect upon the apparent digestibility of food have already been discussed. (See pages 148 and 196.) By its very presence in the air of the respiration chamber or in the samples of air expired from the trunk, this gas complicates the actual gas analyses and the calculations of the results of the same. Thus far in the discussion of the measurements of the products of respiratory exchange by the elephant consideration has been given to the presence of methane only from the mechanical and mathematical standpoints, that is, from the standpoint of actually measuring it by means of the gas-analysis apparatus, correcting for its presence in the gas sample when calculating the oxygen deficit and the apparent respiratory quotient, and calculating the volume of methane production from the total ventilation rate and the percentage of methane in the gas sample. In other words, if 100 liters of methane had been introduced into the respiration chamber from an outside source, the measurement of the volume of this gas escaping in the air leaving the chamber would be given no different treatment from that given to the measurement of the methane actually produced inside the paunch of the animal and excreted inside the respiration chamber. The next matter for consideration (the production of methane by the elephant having been demonstrated and its volume measured) is as to what influence the methane production has upon the interpretation of the respiratory exchange measurements, especially as expressed in terms of carbon-dioxide production, the respiratory quotient, and the heat production.

The intensive fermentations taking place in the intestinal tract of Herbivora, particularly ruminants, result not only in the production of large amounts of methane but of still larger amounts of carbon dioxide. It is a question whether the fermentative processes are wholly anaerobic or not. Probably there is not a great absorption of oxygen accompanying these processes. When the length of stay of food in the intestinal tract is short, as for example with the dog or the fowl, there is little, if any, intestinal fermentation, there is little heat production resulting from bacterial processes, and the entire transformations arise from tissue cellular metabolism. When the length of stay of food in the intestinal tract is prolonged, however, as in the case of the large ruminants, there is considerable intestinal fermentation and here all the gaseous products do not arise from true body metabolism. One may look upon the contents of the intestinal tract of the elephant or any other herbivore in which there is a large residuum of food as an enormous incubating oven maintained at about 38° C., that is, under ideal conditions for bacterial development. The chief fermentation is apparently that of carbohydrate and cellulose, during which large quantities of carbon dioxide are given off and considerable quantities of methane are produced. In a sense this same fermentative action might take place if the entire contents of the intestinal tract were placed, for example, in an electrically controlled incubating oven. The processes directly ascribable to such bacterial or fermentative action are extra-cellular and not a part of the tissue metabolism of the body.

An animal such as a steer or an elephant thus has two distinct types of disintegration processes going on within the body, one the purely fermentative and the other the true tissue metabolism. The relative proportions of the intensity of these two processes are indicated by the relationship between the methane produced and the carbon dioxide produced. However, as a certain amount of carbon dioxide invariably is associated with methane production, the comparison may not be directly made. There should be, theoretically, a consideration of the carbon dioxide specifically accompanying methane as distinguished from the entire carbon dioxide as given off by the animal. It is relatively simple to measure the amount of methane eliminated, but it is impossible to differentiate by gas analysis between the carbon dioxide produced by fermentation and the carbon dioxide produced by oxidation during true destruction of metabolites. To enable this differentiation several studies employing various techniques have been undertaken, and an attempt has been made to establish the relationship between the methane production and the carbon dioxide produced by fermentation. Thus, Markoff [1] and Krogh and Schmit-Jensen [2] have studied the fermentation gases of the contents of the paunch and intestinal tract after removal from the body of the animal. Klein [3] and Møllgaard and Andersen,[4] on the other hand, have employed a closed-circuit respiration chamber and the tracheal cannula method to measure separately the gases escaping through the anus and the pulmonary gases. The ratios of methane to carbon dioxide found by these investigators vary considerably, but undoubtedly those established by Krogh and Schmit-Jensen and by Møllgaard and Andersen, namely, 1:2.6 and 1:2.8, can be accepted as indicating with reasonable accuracy the volume of the carbon-dioxide production accompanying the production of methane. If it is assumed that for every liter of methane 2.6 liters of carbon dioxide are formed in fermentation, then if the methane production is accurately determined, it is possible by the use of this ratio to compute the carbon dioxide of fermentation. This proportion of carbon dioxide ascribable to fermentation must be deducted from the carbon dioxide as measured, to correct for fermentation products. This corrected carbon dioxide is, however, split in calculations to the protein and the non-protein carbon dioxide, as in the calculation of the non-protein respiratory quotient. From the results of these final corrections the heat production of the animal itself, as distinguished from that of the fermentative processes, may be calculated. These calculations have in this report, however, only a secondary interest to the main consideration of the energy metabolism, and it is with the influence of the fermentation processes upon the calculation of the energy metabolism that we are more particularly concerned.

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[1] Markoff, J., Biochem. Zeitschr., 1913, **57**, p. 1.

[2] Krogh, A., and H. O. Schmit-Jensen, Biochem. Journ., 1920, **14**, p. 686.

[3] Klein, W., Biochem. Zeitschr., 1916, **72**, p. 169.

[4] Møllgaard, H., and A. C. Andersen, D. Kgl. Veterinaer og Landbohøjskole, Aarsskrift, Copenhagen, 1917; Andersen, A. C., Biochem. Zeitschr., 1922, **130**, p. 143.

Respiratory Quotients as Affected by Corrections for Protein, Methane, and the Carbon Dioxide of Fermentation

It will be recalled that in the three trunk-breathing experiments the apparent respiratory quotients were 1.07, 1.06, and 1.11. On the other hand, in the respiration chamber experiments the apparent respiratory quotients ranged from 0.95 to 1.06 (see table 41) and averaged 1.01. It might be idle speculation to attempt an explanation of this relatively slight difference in quotients. It is our judgment, however, that the relatively slight differences in the second decimal place in the apparent respiratory quotients obtained by the two methods of measurement are not of great significance other than that they indicate that Jap was definitely in the digestive and absorptive state.

The respiratory quotients discussed above are all indicated as "apparent" respiratory quotients. For many physiological interpretations, it is desirable to know that portion of the gaseous metabolism that is participated in by material other than protein. From the nitrogen excretion in the urine the amount of protein involved in the metabolism is computed. From this and from the known amount of oxygen required to oxidize a gram of protein and the known amount of carbon dioxide resulting from such oxidation, it is possible to compute the volumes of carbon dioxide and oxygen involved in the oxidation of the protein metabolized. These volumes are deducted from the total volumes of carbon dioxide and oxygen as measured, and the volumes left are ascribable to the combustion of non-protein material, that is, to carbohydrate and fat. The ratio between these corrected volumes represents the non-protein respiratory quotient. By this method of calculation the non-protein respiratory quotient is 1.03, that is, 0.02 greater than the average apparent respiratory quotient. (See table 42, page 265.)

The use of the non-protein respiratory quotient of itself suggests an attempt to sharpen and clarify information as to the nature of the combustion processes. It so happens, however, that with the elephant and even more so with the ruminants another factor enters, which is disturbing and not so simple to calculate, that is, the production of rather considerable amounts of fermentative products, chiefly methane, and an accompanying moiety of carbon dioxide. The fact that the discharge of these fermentation gases through the trunk and through the anus is unequal emphasizes the uncertainty in comparisons of the results of trunk-breathing experiments with the results of experiments by the respiration chamber technique, which measures the gaseous emanations from all parts of the body. These two fermentation gases, methane and carbon dioxide, each introduce their own specific error into the calculation of the respiratory gases and the interpretation of the results. The methane factor is fairly readily determined, but the fact that a relatively considerable amount of carbon dioxide, ordinarily assumed to have been produced by the cell metabolism of the animal, is, as a matter of fact, produced by fermentation changes, makes it necessary, in order to obtain the true cellular metabolism, to attempt apportionment of the gaseous exchange between the metabolism of fermentative changes or infusoria, on the one hand, and the true cell metabolism, on the other.

According to Andersen's method of calculating the heat production, the assumption is made that the methane is completely burned, and hence both the non-protein carbon dioxide and the non-protein oxygen are corrected for the carbon dioxide and oxygen taking part in the combustion of the methane. Under these conditions a corrected non-protein respiratory quotient is found averaging 0.05 lower than the non-protein quotient of 1.03. According to the method employed by Krogh the carbon dioxide of fermentation (calculated by multiplying the measured methane production in liters by the factor 2.6) is deducted from the non-protein carbon-dioxide value and the result is divided by the non-protein oxygen value. The quotients as computed on this basis range from 0.87 to 0.92. It is difficult to find any criticism of the mathematics of either of these methods and yet it seems impossible that an animal subsisting almost solely upon a carbohydrate-rich material and fed essentially at a maintenance level or possibly a little above could have a respiratory quotient in the neighborhood of 0.90 or even lower. This seems to us a serious challenge of the Krogh method of making these calculations. It furthermore raises the question, if the correctness of the method of calculation is assumed, as to whether there may not be a certain amount of oxygen participating in the fermentative action. As is well known, in studies of the gaseous metabolism of Herbivora the lability of the carbon-dioxide excretion can hardly be overestimated, since the neutralization of carbonates, for example, liberates large amounts of carbon dioxide.

The relationship between the apparent respiratory quotient, the non-protein respiratory quotient, and the corrected non-protein respiratory quotient (this latter meaning the quotient with presumably justifiable corrections for the gaseous emanations due to the fermentation processes) has without doubt a general theoretical interest. From the practical standpoint the respiratory quotients are not of great importance. In the first place, it is known that Jap was fed almost exclusively a carbohydrate diet. Consequently it is to be expected that for the most part she would be burning carbohydrates with but a small proportion of protein, and one would normally look for a respiratory quotient of not far from 1.00 or a little below. Hence the respiratory quotient as an index of what the animal was actually burning would not, *a priori,* be startlingly informative.

The respiratory quotient is commonly of value in computing the energy output from the measured oxygen consumption, the caloric value of which is indicated by the quotient. Jap's oxygen consumption was measured. What shall be the caloric value of oxygen used for calculating the probable heat production from this measured oxygen consumption? At the worst we have to consider the possibility that the respiratory quotient may range from only 1.00 to 0.70. The caloric value of a liter of oxygen at 1.00 is 5.047. The caloric value at a quotient of 0.70 (which is not conceivable with an animal on full feed) is 4.686 or 7 per cent lower than that at a quotient of 1.00. If the common custom employed in experiments with humans is followed, of assuming a respiratory quotient of 0.82 with an energy value of 4.825 calories per liter of oxygen, the difference would not be over ± 4 per cent. The nature of Jap's food and the fact that she was on a maintenance level justify the assumption that the respiratory quotient was between 1.00 and 0.85 and more probably between 0.90 and 1.00. The error of assuming a quotient of 1.00 or of 0.90 would not affect the calculation of the heat production from the oxygen consumption by more than 2 per cent. Consequently the respiratory quotients in these experiments with Jap are in large part a matter of academic rather than of practical interest.

From the purely academic standpoint one can, with great propriety, discuss the respiratory quotient as related to the fact that there is a considerable amount of fermentative action accompanied by a large production of carbon dioxide, probably unaffected by any significant absorption of oxygen. This fact has led to attempts on the part of various writers to analyze the respiratory gases on the basis of what proportion can be ascribed to bacterial or fermentative action and what proportion more legitimately belongs specifically to tissue metabolism. Various methods of computing these relationships have been presented, based upon (1) the proportion of methane to carbon dioxide, (2) the relationship of methane produced to the amount of carbohydrate digested, (3) the ratio of methane to the amount of crude fiber digested, (4) the number of calories liberated for each gram of methane produced, chiefly determined by experiments *in vitro,* (5) the assumption that no methane is formed, and (6) the assumption that the methane as formed is completely burned with the resultant production of carbon dioxide and water, making necessary subsequent deduction for the actual energy in the methane given off. All these academically interesting calculations may be, with propriety, considered here, although they do not play any great rôle in the calculation of the probable energy output. With ruminants more weight has been laid upon these calculations. Since, however, many of them have been based solely upon the exhalation of methane through the mouth and nose and disregard completely the exhalations through the anus, they can be of only relatively slight value.

HEAT PRODUCTION

In lieu of direct calorimetry, the observations have had to be made by indirect calorimetry and, as already stated, the fermentation processes render the calculations based upon indirect calorimetric measurements complicated. Even direct calorimetry would not much simplify the problem, for by this method one would be measuring the sum total of the heat production of the animal plus the heat resulting from the fermentation processes without (as is the case in gaseous metabolism measurements) any index as to the heat of fermentation. No one has given any more attention to this subject than has Krogh, who has especially studied the fermentation processes. Krogh's method of calculating the heat production from the measurements of the respiratory exchange aims at excluding the heat of fermentation. For this reason he deducts from the carbon-dioxide production as measured (corrected to the non-protein basis) 2.6 liters of carbon dioxide for each liter of methane produced. The difference is then divided by the oxygen consumption (corrected to the non-protein basis), to obtain the "true respiratory quotient for the organism itself." The heat production is finally calculated from the corrected values for oxygen consumption and respiratory quotient by the use of the Zuntz formula: $O_2 \times$ [4.686 + (true non-protein R. Q. — 0.707) 1.23].

Møllgaard and Andersen assume in their calculations that the methane is completely burned. They, therefore, increase the carbon-dioxide production as measured by one volume of carbon dioxide for every volume of methane produced and the oxygen consumption as measured by two volumes of oxygen for every volume of methane produced, and then calculate the heat production from the corrected oxygen value and the corrected respiratory quotient according to the Zuntz formula, making also the usual correction to the non-protein basis. The heat production thus computed is increased for the heat produced in the oxidation of protein, and from this result is deducted the heat of fermentation (on the assumption that each liter of methane results in the production of 9.565 calories). The final result represents a combination of tissue metabolism and metabolism of infusoria. For purposes of practical feeding of animals, obviously it is necessary to give the animal enough food for its own vital processes as well as its parasites or, specifically in the case of the bacteria, enough to provide for the destructive losses incidental to fermentation.

It has been found repeatedly, both in experiments with the bomb calorimeter and in respiration calorimeter experiments with large animals, that the caloric value of oxygen remains singularly constant at about 5 calories per liter, irrespective of the kind of material burned. Hence a true measurement of the oxygen consumption should be, *a priori,* a satisfactory measure of the heat production. The heat production of Jap has been calculated according to the methods of Krogh and Møllgaard and Andersen and also according to the usual method of calculating the heat production of an animal from measurements of the respiratory exchange when there is little or no intestinal fermentation, that is, by multiplying the oxygen consumption as measured by the caloric value (in this case 5.047 calories per liter) indicated by the apparent respiratory quotient. Comparison of the results (see table 42) indicates that the Møllgaard and Andersen method gives values approximately 1 per cent lower and the Krogh method values about 3 per cent lower than those obtained when no attempt is made to correct for the products of fermentation. With most other animals except the large ruminants, the fermentation factor plays relatively a small rôle in indirect

Table 42—*Calculation of heat production from respiratory exchange measurements on the elephant Jap (average values per 24 hours)*

Date	As measured			Non-protein basis[2]			Methane[3]	Andersen method				Krogh method			Heat production calculated from O_2 (as measured) at caloric value of 5.047 [11]
	CO_2	O_2[1]	Apparent R. Q.	CO_2	O_2	R. Q.		Non-protein CO_2 corrected for methane [4]	Non-protein O_2 corrected for methane [5]	Corrected non-protein R. Q. [6]	Heat production [7]	CO_2 of fermentation [8]	Corrected R. Q. [9]	Heat production [10]	
1935	liters	liters		liters	liters		liters	liters	liters		cal.	liters		cal.	cal.
Mar. 10	13,162	13,032	1.02	12,043	11,643	1.03	501	12,544	12,645	0.99	63,700	1303	0.92	62,400	64,100
Mar. 11	13,349	13,219	1.00	12,230	11,830	1.03	510	12,740	12,850	.99	64,600	1326	.92	63,300	65,000
Mar. 12	13,738	13,608	1.00	12,619	12,219	1.03	661	13,280	13,541	.98	66,500	1719	.89	64,800	67,000
Mar. 13	13,378	13,248	1.02	12,259	11,859	1.03	665	12,924	13,189	.98	64,600	1729	.89	63,000	65,200
Mar. 14	13,838	13,694	....	12,719	12,305	1.03	758	13,477	13,821	.98	66,800	1971	.87	64,900	67,400
Mar. 14	15,250	15,106	....	14,131	13,717	1.03	746	14,877	15,209	.98	74,000	1940	.89	72,100	74,500
Mar. 15	13,882	13,738	....	12,763	12,349	1.03	742	13,505	13,833	.98	67,100	1929	.88	65,200	67,600

[1] Average CO_2 as measured divided by average apparent R.Q. of 1.01.

[2] Assumed urinary nitrogen excretion of 235 gm. per day multiplied by factors of 4.76 and 5.91 for CO_2 and O_2, respectively.

[3] See explanation of method of calculation given on page 256.

[4] CO_2 on non-protein basis + (1 × volume of methane).

[5] O_2 on non-protein basis + (2 × volume of methane).

[6] Corrected non-protein CO_2 divided by corrected non-protein O_2.

[7] Non-protein O_2 corrected for methane [4.686 + (corrected non-protein R.Q. − 0.707) 1.23] + calories from oxidized protein − calories from combustion of methane − 1700 calories for keeper. Calories from oxidized protein calculated by multiplying 235 gm. urinary nitrogen per 24 hours by protein factor 6.25 and by factor 4.4 calories per gram of protein. Calories from methane calculated by converting liters of methane to grams (0.7168 gm. per liter) and multiplying by factor 13.344 calories per gram.

[8] Methane production times 2.6.

[9] (Non-protein CO_2 − CO_2 of fermentation) ÷ non-protein O_2.

[10] Non-protein O_2 [4.686 + (corrected R.Q. − 0.707) 1.23] + calories from oxidized protein. Deducted 1700 calories for man.

[11] 1700 calories deducted for man.

calorimetric measurements, and even with the large ruminants fermentation practically disappears by the fourth and fifth days of fasting, the time when basal metabolism measurements on these animals are ordinarily made.

If an attempt is made to correct for the metabolism of the infusoria with an animal on feed, it is seen that by the Krogh method the correction is of the order of 3 per cent. Since all basal metabolism measurements are made with animals in the post-absorptive condition, this correction would not enter into the calculation under ordinary conditions. However, when one must measure the metabolism of an animal on feed and attempt to compute therefrom the metabolism without feed, this factor can not be wholly disregarded. But since the correction in the heat production of a cow on full feed is, by the Krogh method, only of the order of 3 per cent, it has not been deemed necessary to attempt to make this correction in estimating the heat production of the elephant Jap. As a matter of interest, the calculations have been carried out by both the Andersen method and the Krogh method, as shown in table 42. Since the differences in the heat values calculated by these two methods are so small and the results agree, for the most part, so well with the calculations from the measured oxygen consumption (see last column of table 42), all subsequent discussions of the heat production of Jap will be based on the calculations from the oxygen consumption as measured and an average respiratory quotient of 1.01.

It was not a matter of vital interest in the study of Jap to know precisely what the true respiratory quotient was. With an animal subsisting almost exclusively upon carbohydrate, as was Jap (being fed hay only), one would expect a combustion predominantly of carbohydrate, and consequently the finding of an apparent respiratory quotient above 1.00 would be quite in line with what would be expected. This was another reason for the decision not to use the Andersen method of calculation.

The oxygen consumption was not measured with Jap in each individual period on the different experimental days, but it has been argued that since the average apparent respiratory quotient was always so close to 1.00 and since the period values for carbon-dioxide production on any given day are so regular, the average oxygen consumption can be computed by dividing the average carbon-dioxide production on the given day by the average of all the determinations of the apparent respiratory quotient, namely 1.01. The results for oxygen consumption thus obtained were then multiplied by the factor 5.047. Since it was necessary for the keeper to remain in the respiration chamber with Jap during the metabolism measurements, obviously the total heat production as thus calculated must be corrected for the heat production ascribable to the man. The presence of the keeper inside the chamber admittedly introduced an error in the technique. But calculation of the total probable metabolism of the man (a calculation that can be made with a maximum error not greater than 25 per cent) showed that it would be relatively insignificant in comparison with that of the elephant, at the most hardly 2 per cent of the total measured metabolism. Keeper Dumont weighed 75.6 kg. He was seated for the most part during the experiments, reading, occasionally calling to Jap and, with one arm, tossing bread to her. An arbitrary assumption has been made that the probable 24-hour heat production of this man while sitting quietly would be 1700 calories, and this value has been deducted from the values calculated for the total heat production of elephant plus man to obtain the total heat production of the elephant alone. Even if the estimate of 1700 calories as the heat production of the keeper were changed considerably, it would not alter significantly, percentagewise, the final calculation of the total heat production of the elephant. Hence the results computed as explained above (see the last column of table 42), although not indicative of Jap's basal metabolism, may be considered to represent her 24-hour heat production under conditions of quiet standing, with a minimum amount of muscular activity incidental to the eating of small amounts of hay and bread. These values will be used in the immediately following discussion. The corrections to be made in these values to approximate the probable basal metabolism of the elephant will be considered later. (See page 277.)

Total Heat Production

Interest in the metabolism of Jap, as measured by the respiration chamber experiments, centers first in the heat production of the animal as a whole, for the purpose of comparison of the results by the two different methods of measurement (chamber and trunk breathing), for comparison with the earlier data obtained by Brody, and for the attempt to establish the energy balance of Jap. The total 24-hour heat production of Jap varied on the seven days of measurement in the respiration chamber from a minimum of 64,100 to a maximum of 74,500 calories. There is no obvious explanation for the maximum value. If one disregards this, the values range only from 64,100 to 67,600 calories, and the average value of 66,100 calories is probably more truly indicative of the total metabolism of this animal. If the lowest values are used, on the ground that metabolism measurements are always above rather than below the basal level, the well-agreeing minimum results on March 10, March 11, and March 13 show a round average of 64,800 calories, which may be accepted as representing the probable standard (standing, on feed, and minimum activity) metabolism of this animal, although by no means basal. *The average of 45,800 calories obtained in the trunk-breathing experiments is 29 per cent lower than this, a difference which proves the inadequacy of the trunk-breathing experiments for measuring the metabolism of the elephant* and indicates that undoubtedly there was a loss of respiratory products through the mouth. Hence in any further consideration of the metabolism of the elephant on any basis whatsoever, whether expressed as total heat production or heat production per unit of weight or surface area and whether corrected for the influence of food ingestion or not, all trunk-breathing experiments must be disregarded. The real value of the trunk-breathing experiments, therefore, is restricted to the positive information that they give regarding the character of the respiratory quotient, the presence of methane in the expired air, the respiration rate, and the ventilation of the lungs, information that is of itself valuable and that more than compensates for any inability to compute the heat production from the gaseous metabolism thus measured.

Although there is a systematic loss of approximately 30 per cent in the trunk-breathing measurements, because of the mouth breathing, the results of these experiments have actually been used in our discussion in at least two ways, first, in comparing one period measurement by Brody on Jap with our several findings on Jap in trunk-breathing experiments. Secondly, use has been made of the fact that three elephants of substantially the same body weight (3600 to 4000 kg.) showed approximately the same total heat production when measured by Brody. This suggests that Jap, one of the three measured by Brody and the animal measured by us, was in all probability a normal animal and compared favorably with two other animals of similar size.

Since the accuracy of the respiration chamber technique is beyond question, the conclusion is that the *standard metabolism of an elephant of the size of Jap (3672 kg.) is 64,800 calories per 24 hours.*

The enormous heat production of the elephant can be visualized when one considers that the metabolism of each elephant would represent the heat production of approximately thirty men. Thus in the elephant barn in Florida where thirty-four elephants were brought together, the heat developed by these animals would be the equivalent of that produced by a regiment (1000 men). A striking illustration of this heat production was shown on one rather chilly night, when the canvas curtains in front of the elephants were lowered to keep out the chill.[1] The outdoor temperature was 15° C. The temperature inside the canvas curtains (*i. e.*, just in front of the elephants) at about 4 feet from the ground was 25° C. Thus the heat developed by these animals in the poorly insulated shed resulted in a temperature inside the elephants' enclosure 10° C. higher than the outdoor temperature.

From the standpoint of size it is interesting to compare the standard total heat production of the elephant, the largest animal whose metabolism has been measured up to the present date, with the greatest standard heat production of the largest animals heretofore studied. At the Agricultural Experiment Station at Durham, New Hampshire, Professor E. G. Ritzman has found that the total heat production of a cow or a steer, when on food, is by no means proportional to the body weight alone but is largely proportional to the amount of the intake. The larger the intake, the larger the heat production. This indicates the tremendous stimulus, to the metabolism, of food of a carbohydrate nature. At Durham a cow on full feed, in full milk production, weighing 612 kg., measured in two consecutive 12-hour periods while lying and standing at will, was found to have a total 24-hour heat production of 18,700 calories. Thus the elephant, which was receiving only a maintenance hay ration, weighed six times as much as the cow and yet had a heat production only about three and one-half times as great as that of the cow fed to the full limit for milk production. It may be argued that the comparison should more strictly be made with animals receiving, like Jap, a maintenance hay ration. Under such conditions of feeding the metabolism of the cow would be about 13,000 calories or one-fifth that of the elephant. This is more nearly what one would expect in proportion to the size. On the other hand, a Percheron mare weighing 600 kg., on a presumably maintenance ration of hay and grain, has been found to have a total heat production of 22,000 calories. In this case the elephant weighed six times as much as the horse and yet its heat production was only about three times as great. In view of the difference in size, therefore, Jap's standard total heat production is relatively lower than that of the cow and the horse on full feed.

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[1] A good illustration of the extreme care taken to prevent the elephants from becoming chilled. To a tropical animal 15° might be chilly, and protection against this very moderate lowering of temperature was taken.

Influence of Environmental Temperature

Jap was measured at temperatures of from 20.0° to 24.7° C. during the respiration chamber experiments. Experience with other animals has shown that the environmental temperature for 24 hours previous to the period of measurement should be the same as that prevailing during the measurement, since there is a lag in the temperature effect.[1] This particular feature of temperature regulation could not be controlled in the experiments with Jap. The barn could not be heated to 20° or 24° C. and kept at that temperature for twenty-four hours before the measurements, and twice the temperature was as low as 0° C. during the night (see table 41). The data obtained give no true knowledge with regard to the temperature reaction of the elephant. While the trunk-breathing experiments were being made, the barn temperature was from 16° to 18° C., that is, lower than the environmental temperature during the chamber experiments. Yet the trunk-breathing experiments showed a lower metabolism than the chamber experiments. If it could be assumed that the trunk measurements represent the total metabolic activity of the animal, one would have expected a higher metabolism on the day when these measurements were made, because of the lower environmental temperature. The picture is by no means clear.

Normality of the Elephant Jap

Either by accident or design, Jap was exposed to an environmental temperature considered abnormal for elephants, and yet she apparently thrived under such treatment. This exposure to low temperatures had been her lot for a number of years and was not a recently superimposed factor. The question arises as to whether Jap, by reason of her repeated exposure to cold, has not a metabolism peculiar to her as an individual? Perhaps with other elephants the total heat production might not be found to be the same as that of Jap. It is unfortunate that respiration chamber measurements were made only on this one elephant. Fortunately, however, Brody measured (in trunk-breathing experiments, to be sure) the metabolism not only of Jap but of two other elephants of about the same size (Nos. 51 and 52). Although it has been pointed out that the trunk-breathing measurements are nearly 30 per cent lower than the respiration chamber measurements, Brody's heat values for Nos. 51 and 52 agree fairly well with one of his three values obtained with Jap and with the three values obtained by us on Jap in the trunk-breathing series. Consequently, if there is anything approximating a systematic error in the technique of trunk-breathing measurements, this comparison is good evidence that Jap's metabolism is characteristic of that of other elephants of her size and is not peculiar to her alone. This is in full conformity with the fact that all the other physiological observations made on Jap were found to be in agreement with those made on other large elephants.

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[1] Gelineo, S., Annal. de Physiol., 1934, **10**, p. 1083.

Belief that Jap's metabolism is not abnormal because of her exposure to cold temperatures is supported by the data obtained by the Nutrition Laboratory on the artist's model, Miss W., who was found to withstand cold extraordinarily well without shivering, and whose basal metabolism, when studied under ordinary conditions as to clothing and in the zone of thermic neutrality, was no higher than that of other women of her age and size. It is believed that if Jap had been measured below the zone of thermic neutrality, which for her may be very wide, she would have had a much higher metabolism. Her highest heat production on any day (March 14) was 74,500 calories, when the chamber temperature was 21.5° C. or 1.3° C. higher than it was on the day (March 10) when the lowest heat production was noted. It is thus highly probable that an environmental temperature of 20° C. was in her case not below the zone of thermic neutrality. On March 10, however, Jap wore a blanket during the experiment, and this blanket might have played a rôle in lowering her metabolism. Against this conclusion is the fact that on March 11, when the blanket was not worn but when the chamber temperature was the same as on March 10, the heat production was but 1.5 per cent higher. It is, therefore, believed that the blanket worn on March 10 was without significant effect and that the temperature of 20° C. was not below the zone of thermic neutrality.

Although the elephant is a hairless animal and hence insufficiently protected with heat-insulating material, little is known with regard to the true heat-insulating effect of the enormously thick skin and the subcutaneous tissue. Prehistoric elephants were, without doubt, fairly heavily furred, particularly the mammoths, but their geographical range was into areas of intense cold (upper Siberia) and hence the added fur protection was essential for these extremes.[1] Practically all the large hairless mammals—the elephant, the rhinoceros, the hippopotamus—are tropical animals. The elephant, although primarily designed for tropical or warm environments, might conceivably be very resistant to cold with a heavy fur coat. It is a matter of no little interest that Jap, an elephant that had had, so far as is known, the most severe training in the "hardening processes," showed no appreciable development of new hair. In other words, there was no indication of an increased growth of hair stimulated by the cold environment, a phenomenon noted with most other animals.[2]

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[1] A most complete study of the hair, both of the mammoth and of the modern elephant, has been presented with meticulous care by K. Möbius (Sitzungsb. d. konigl. preuss. Akad. d. Wissensch., Berlin, 1892, p. 527).

[2] Although the elephant is essentially a hairless animal, it has a sparse coating of stiff, but wholly unprotective hair. For æsthetic purposes elephants are singed prior to their going "on the road" in the spring. Thus the hair is burned down to a short stubble. Since the singeing process can not be used in the delicate ear, the hair in the ear is closely clipped. On November 20, 1935, when the Ringling elephants had just finished their long spring, summer, and early fall tour, their hair had, in general, grown out to a length of about 20 mm. and the hair in the ear had grown to nearly twice this length. Although, therefore, in this period of several months on the road there was a growth of hair, this certainly can not be considered in any sense of sufficient density or length to provide any means for resisting cold environments.

From all these considerations it is apparent that Jap's acquired resistance to cold had not changed her metabolism from that found with other elephants of approximately the same weight. It is a matter of regret that her metabolism could not have been measured after she had spent several hours at an environmental temperature of 0° C. This was impracticable, and hence her reaction to this low temperature is unknown. The fact that Jap withstood the exposure to extreme cold is not at all out of harmony with the fact that elephants, in their earlier days at least, were widely distributed and were found in the Barbary States at an altitude as high as 10,000 feet. It is surprising, therefore, that the present-day tendency of elephant trainers in large circuses is against any undue exposure to chilling winds or drafts. This is undoubtedly based upon probably sad, if not bitter, experience. In general, one thinks of elephants as coming from tropical climes. Hence *a priori* one would consider that they should be provided with as nearly as possible a tropical or sub-tropical environment. The best and most intelligent elephant trainers undoubtedly attempt to do this. The fact remains, however, that Jap has been subjected to a great deal of cold throughout her life and yet has succeeded in arriving at the age of forty years in good health and with a physiology that, so far as it has been possible to assess it by the various measurements made, is normal.[1]

ENERGY BALANCE

The respiration chamber experiments indicate that the total daily heat production of Jap was 64,800 calories. This is based upon measurements when the animal was standing quietly and eating hay and bread, and does not represent periods of complete muscular repose, which periods do not occur with the elephant except during deep sleep. No measurements were made when Jap was lying down, asleep. Doubtless during sleep the metabolism would have been somewhat lower, possibly 10 per cent lower, during the few hours when the elephant normally sleeps. The value of 64,800 calories can be considered, however, as representing Jap's total energy needs during an ordinary 24-hour period when not performing external muscular work, but not corrected for the short period of sleep, when the energy needs might be somewhat lower.

The question arises as to whether the food intake of Jap met her energy needs. Under ideal conditions (which, in Jap's case, did not exist) the energy balance should be determined by measurements of the daily energy intake over a long period of time, preferably several weeks, with measurements of the standard metabolism (standing quietly and not post-absorptive) during the same period. In lieu of such simultaneous measurements there are available for comparison the observations on the standard heat production calculated from the measured oxygen consumption, the excretion of methane during the 6-day period in March, and measurements of the total food intake, the total fecal output, and the urinary excretion (unfortunately not completely collected) during a 9-day digestion period nearly a month later. Therefore, if the imperfect method is employed of comparing energy intake with energy output as measured at two different times and not simultaneously, Jap's energy balance can at least be approximated. During the nine days when the food intake was measured (see table 22, page 164) the energy value of the hay eaten per day amounted to 206,500 calories. This can be considered as the total daily intake, without any attempt to correct for the small amount of energy in the bread fed during the particular hours when the respiration chamber experiments were in progress. During these same nine days the daily energy output in feces amounted to 123,861 calories. An estimation of the energy value of the urine has been made by assuming an average nitrogen output in the urine of 235 grams per day (see page 217) and an energy value of 35 calories per gram of urinary nitrogen, based on direct determinations of the energy in Jap's urine. (See table 38.) On this basis the daily energy outgo in urine would be 8225 calories. From the respiration chamber experiments it can be assumed that 655 liters of methane were excreted per day. At the rate of 13.344 calories per gram of methane, the energy represented by the methane would be 6265 calories per day. The total energy outgo in feces, urine, and methane would thus be 138,351 calories. The standard daily heat production of Jap averaged 64,800 calories. Hence the total energy outgo was 203,151 calories, as compared with the average daily intake in hay of 206,500 calories. On this basis Jap was gaining *ca.* 3350 calories per day, that is, her energy intake was 1.6 per cent greater than her energy output. This indicates that she was on slightly overmaintenance rations. Unfortunately too much weight can not be laid upon this indication of slight over-nourishment, because the two assistants who aided in the 9-day digestion experiment thought that Jap had been underfed at the time of the previous series of observations and hence were inclined to favor giving her a modest extra allowance of hay whenever opportunity occurred during the digestion trial.

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[1] Benson's remarkable animal, No. 4, is (according to her keeper, Neuffer) taken out of the elephant house frequently in the winter, and she is not protected with a blanket. According to Hagenbeck, "no fallacy is more wide-spread than that wild animals have to be kept throughout the winter carefully guarded from the effects of the low temperature. In Stellingen we keep lions, tigers, giraffes, ostriches, and other tropical animals wandering freely about in the open, though they always have access to cover if they should wish for it." (See the translation of Hagenbeck's book on "Beasts and Men" by H. S. R. Elliot and A. G. Thacker, London and New York, 1909, p. 202.) A most singular instance of protecting an elephant from severe cold is that recorded by J. Schiött (Zool. Garten, 1905, 46 Jahrg., p. 10). An elephant was taken in a menagerie to Ström, Sweden, as far north as 64°. During the stay there the temperature ranged from -12° to -20° C. The trainer provided the elephant with a coat of reindeer skins and some sort of shoes. It is stated that the elephant returned from this trip with only a slight freezing of the external genitalia and recovered in complete health. The article is accompanied by a photograph showing the animal with its fur coat, a photograph that has been reproduced by Hagenbeck in his book on "Beasts and Men" (see page 156).

METABOLIZABLE ENERGY

The metabolizable energy, that is, the total daily energy intake less the daily energy outgo in feces, urine, and methane, has been calculated from the values cited in the preceding paragraph to be 68,149 calories. Since the energy intake amounted to 206,500 calories per day, but 33 per cent was metabolizable. As already pointed out in the calculation of the digestibility of the hay, the elephant has a particularly poor digestion and gets less out of its hay on the energy basis than any other animal that has been studied. The metabolizable energy, however, does not represent the actual amount of energy available to the animal for purposes of living, growth, and deposit, because the very fact that food is ingested results, particularly in Herbivora, in a greatly increased metabolism. This increase, which has been termed the specific dynamic action, represents an excess energy expenditure resulting from food intake. Hence, although for every 10 calories ingested in the form of hay the elephant can actually absorb 3.3 calories, of these 3.3 calories only a part is available for basal needs, deposit or growth, owing to the stimulus to heat production resulting from the food. In other words, an enormous loss of energy ensues in the various steps from the intake of energy to the actual use of the energy of intake in true basal tissue metabolism. This fact is of particular importance with domestic animals, the main object of feeding which is either for milk production or deposit of meat material. This consideration of the metabolizable energy, in conjunction with the earlier discussion of the digestibility of the hay, emphasizes still further the poor economy of the elephant's digestive and assimilative system. No animal with which the Nutrition Laboratory is familiar has a poorer utilization of its food material than has the elephant.

The very process of gathering its food material in the wild must be an expensive one for the elephant. This animal travels great distances, must uproot material or pull down branches and strip off leaves. It engages in much more vigorous activity during the process of browsing than does the ordinary domestic animal at pasture. Hence the cost of living of the elephant must be very great when it feeds only upon what it can get from the wild. This fully explains the fact so often noticed by those hunting elephants in the wild, that a great area of forest or grazing land is destroyed, trampled, or beaten down by these animals in their search for sufficient food to keep their bodies in energy equilibrium, to say nothing of the enormous food needs during the period of growth. Since the 24-hour energy output of the elephant, certainly in captivity, must be met by an equivalent amount of metabolizable energy either from pasturage or from food fed by the owner, one is not surprised that very large amounts of food are necessary.

Water Vaporized and Heat Lost Through the Path of Water Vapor

Because of the large surface area of the elephant's body, one would expect a large loss of water vapor irrespective of the water of respiration given off through the mouth or the trunk. On the other hand, the fact that the elephant's skin is hard and dry would lead to the conclusion that there can not be a great loss of water from the skin, although sweat glands are undoubtedly present. (See page 276.)[1] With the aid of the Carpenter chemical hygrometer [2] it was possible on two days (March 14 and 15) to determine the water vapor given off during the periods of measurement inside the respiration chamber. The technical difficulties in the condensation of water in the tubes leading to the hygrometer prevented accurate measurements on any days prior to March 14.

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[1] In spite of the fact that F. Smith (Journ. Anat. and Physiol., London, 1890, **24**, p. 493) reported the absence of sweat glands in the elephant, Evans (*loc. cit.*, p. 74) states that "sweat glands are situated in the skin, whose function it is to secrete sweat, which by evaporation assists in regulating the temperature of the body. This secretion, however, is slight and best seen after removal of pack-gear." This comment of Evans is confirmed by Doherty's observation, mentioned on page 276.

[2] Carpenter, T. M., Journ. Biol. Chem., 1935, **112**, p. 123.

Method of calculating results—The computations for the water-vapor output were made in the same manner as those for the oxygen consumption or carbon-dioxide production, namely, by multiplying the meter reading (reduced to standard conditions of temperature and pressure) by the percentage of water vapor found in the aliquot sample (corrected for the water vapor in the entering air) by means of the Carpenter hygrometer, and correcting for the change in residual water vapor during the period of measurement. (See page 251.) In these calculations the barometric pressure was not corrected for tension of aqueous vapor and the factor for reduction of the meter reading to 0° C. (dry) and 760 mm. was obtained by referring the uncorrected pressure to the average of the dry bulb temperatures of the air entering and leaving the meter. The total water-vapor output, thus calculated, was corrected for the water vapor ascribable to the man inside the chamber. On the assumption that 25 per cent of the total heat production of the man is lost through the path of water vapor, that this man produced 1700 calories per 24 hours, and that each gram of water vapor eliminated is accompanied by the production of 0.585 calorie,[1] it has been calculated that the 24-hour output of water vapor by the man would be 726 grams.

TABLE 43—*Water-vapor output and percentage of heat lost in vaporization of water by the elephant Jap*

Date	Period No.	Water vapor		Total heat production per 24 hrs.[1]	Heat lost by vaporization of water[2]	
		In outcoming chamber air	Output by elephant per 24 hrs.[1]		Total calories per 24 hrs.	Per cent of total heat production
1935		*p. ct.*	*gm.*	*cal.*	*cal.*	
March 14	1	1.260	24,117	74,756	14,108	18.9
(p. m.)	2	1.181	22,898	75,773	13,395	17.7
March 15	1	1.177	21,050	65,453	12,314	18.8
	2	1.099	19,950	67,924	11,671	17.2
	3	1.125	21,204	67,488	12,404	18.4
	4	1.187	24,372[3]	70,904	14,258	20.1
	5	1.227	21,756	66,616	12,727	19.1

[1] Corrected for heat production and water-vapor output of keeper, as explained above.
[2] Assumed 0.585 calorie per gram of water vapor.
[3] Small amount of urine voided during this period.

The water-vapor measurements obtained under satisfactory conditions on the afternoon of March 14 and on the morning of March 15, along with the measurements of heat production, are recorded in table 43, both sets of results being expressed on the 24-hour basis. The heat production has been corrected for the heat production of the keeper, as explained on page 266. It would have been ideal not to have had any feces passed during the measurements, but this was unavoidable. Although the feces were considerable in weight, they were almost spherical in form and the loss of water from this source could not have been, proportionately, very great.

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[1] Dr. J. D. Hardy, in the laboratory of Dr. E. F. Du Bois at the New York Hospital, told the writer that he believes there may be an error of 2 per cent in this factor.

TOTAL WATER VAPOR FROM LUNGS AND SKIN

In the successive half-hour periods of measurement, two on March 14 and five on March 15, the percentages of water in the outcoming chamber air were extraordinarily uniform, in accordance with the uniformity noted in the percentages of carbon-dioxide increment and oxygen deficit in the chamber air. The water vaporized was also uniform from period to period on both days, with the exception of the fourth period on March 15. During this period a small amount of urine was voided, which fell on the floor and partly vaporized, thus increasing somewhat the water vapor in the air leaving the respiration chamber. On the average there were 22,192 grams representing 27,607 liters of water vapor per 24 hours. This represents the total water vapor eliminated from both lungs and skin.

Percentage of Water Vapor Lost from Skin Alone

The probable relationship between the water vapor lost from the lungs alone and that lost from the skin alone is of interest for comparison with this relationship established for other animals. The mechanics of the loss of water vapor from the elephant's skin is not complicated, as it is with some animals, by the covering of fur or hair. The elephant, however, presents the singular situation of an animal whose nasal passage (trunk) is long. The warm air, completely saturated at the temperature of the lungs, in being exhaled through this tube unquestionably deposits moisture, which one sees continually dripping from the end of the trunk. On the other hand, the air that is inhaled must pass through this long trunk before it reaches the elephant's lungs, so that probably a not inconsiderable amount of vaporization of water may take place before the air enters the lung cavity itself. For these reasons the relationship between the water vapor from the lungs and that from the skin can at best only be approximated, but the calculations have been carried out as follows.

From the trunk-breathing experiments and comparison with the chamber experiments it has been estimated that the probable ventilation of the lungs (reduced to standard conditions of temperature and pressure) by Jap amounted to 310 liters per minute. (See page 121.) The maximum temperature of the expired air (see page 151) was 30.7° C. On March 14 the barometric pressure was 753 mm. The pressure of aqueous vapor in the saturated air exhaled from the trunk, at the maximum temperature of 30.7° C., would be 33.16 mm.[1] Division of this pressure of aqueous vapor by the prevailing barometric pressure indicates that the expired air contained 4.4 per cent of water vapor. The 310 liters of air exhaled from the lungs per minute, therefore, contained 13.6 liters of water vapor at 0° C. and 760 mm.

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[1] Carpenter, T. M., Carnegie Inst. Wash. Pub. No. 303A, 1924, table 3, p. 30.

The air inhaled by the elephant has been assumed to be not air from outdoors but inside the chamber. The animal's head was at the end farthest away from the point where the outdoor air entered the chamber, and it is reasonable to suppose that the air inhaled had nearly the composition of the air leaving the chamber. Hence the percentage of water vapor in the air inhaled has been assumed to be represented by the *average* of the percentage of water vapor in the entering, outdoor air and that in the air leaving the chamber. In the two periods of measurement on March 14 this amounted, on the average, to 1.34 per cent. The 310 liters of air inhaled per minute, therefore, contained 4.2 liters of water vapor. The water vapor exhaled from the lungs is represented by the difference between the 13.6 liters exhaled and the 4.2 liters inhaled, namely 9.4 liters per minute. This amounts to 10,880 grams per 24 hours. Since, on the average, 23,508 grams of water vapor were excreted per 24 hours from both lungs and skin, the water vapor from the lungs alone was 46 per cent of the total water vapor excretion. On March 15 the barometric pressure was 754 mm. and the average water content of the air inhaled during the five periods of measurement was 1.28 per cent. On the assumption that the temperature of the expired air was on this day also 30.7° C. and that the lung ventilation (reduced) amounted to 310 liters per minute, calculation carried out as explained above shows that in this instance 47 per cent of the total water vapor was excreted through the lungs. The average of the two calculations for March 14 and 15 is 47 per cent.

That there is an element of uncertainty in these calculations is recognized. Nevertheless it is clear that no gross error that would affect the calculations by more than 10 or 15 per cent can possibly enter. The conclusion is, therefore, justified that the relationship between the amount of water vapor exhaled from the lungs and that eliminated from the skin is the same with the elephant as with humans. Benedict and Benedict[1] have made separate simultaneous measurements of the water vapor from these two sources with humans and have found that about 50 per cent comes from the lungs and 50 per cent from the skin. It is astonishing that the same relationship is found with the elephant, for the extremely dry, hard skin of this animal, which never feels moist nor damp, and the absence of visible perspiration even when the elephant is working (with the Barnes herd even when the wide harnesses were removed one did not see perspiration under these bands) would suggest that the amount of water vapor lost from the skin would be relatively small.[2] On the other hand, the elephant is a large, hairless animal, which would suggest a large skin loss of water vapor. However, the Nutrition Laboratory found in measurements on a woman that the proportions of water vapor from the lungs and the skin were independent of whether the woman was clothed or nude and whether air was blown over the body at a rapid rate or not. Consequently the significance of the bare skin of the unfurred animal is not so great as would at first appear.

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[1] Benedict, F. G., and C. G. Benedict, Biochem. Zeitschr., 1927, **186**, p. 278; *idem.*, Proc. Nat. Acad. Sci., 1927, **13**, p. 364.

[2] In this connection an observation of Doherty on the Ringling herd of thirty-four elephants is interesting. Once when these elephants were on tour, they apparently received some disturbing factor in the hay fed to them, which resulted in intense perspiration. Water trickled down the sides of the animals, and the blankets with which they were covered were very wet. Unfortunately no records were made of the body temperatures of these elephants, but unquestionably they were in a pathological condition at the time.

HEAT LOST IN VAPORIZATION OF WATER

The determination of the water vaporized from the body of the elephant has a special importance, inasmuch as considerable heat is lost from the body through the path of water vapor. The arrangements at Campgaw did not provide for direct measurement of the heat production of the animal, as would have been the case had a calorimeter been at our disposal. Since each gram of water vaporized calls for the absorption of 0.585 calorie, it is possible, if the total water-vapor output is measured, to calculate the amount of heat lost through this special path, and to note what proportion of the total heat elimination is given off in the vaporization of water. Whatever error may enter into the calculation of the apportionment of the water vapor between that exhaled from the lungs and that eliminated from the skin, it remains a fact that the total water-vapor output was accurately determined and the heat represented by this vaporization of water (0.585 calorie per gram) may properly be referred to the total heat production. This relationship has been calculated for the several periods of measurement (see last column in table 43) and it has been found that, on the average, 19 per cent of the total heat elimination is by vaporization of water. The correct determination of the proportion of heat lost by vaporization of water in the case of other animals has been only too rare. According to the Nutrition Laboratory experience, about 30 per cent of the total heat loss is through the path of water vapor in the case of ruminants, 49 per cent with normal fowl, 25 per cent with man, 17 per cent with the defectively feathered or so-called "Frizzle fowl," and as low as 10 per cent with the hibernating woodchuck. The elephant, therefore, gives off relatively less heat through this path than does man, and although the elephant appears to have an extremely dry skin, with not especially favorable conditions for the loss of water vapor, on the whole a goodly percentage of the total heat disengaged by the animal is lost through this channel. When one considers that the elephant is a large, hairless animal with the skin completely exposed to the air, one is perhaps surprised that an even larger proportion of the heat is not lost by vaporization of water.

BASAL METABOLISM

From the standpoint of comparative physiology, the interest in the measurements of the heat production of the elephant is not to determine the 24-hour energy needs but to compute what is the minimum metabolism corresponding to the so-called "basal metabolism" of other animals. To this end an analysis is necessary of the factors included in the measurement of Jap's metabolism. The elephant in the wild undoubtedly engages in a great deal more physical activity in traveling, searching for and pulling up food, than it does when fed in the ordinary circus or zoological garden. At the same time, even under conditions of feeding in captivity a certain amount of energy is necessary to transport the food to the mouth. The weight of the end of the proboscis is relatively so small in comparison with the weight of the rest of the body, however, that although the proboscis is seemingly in constant action, it does not represent a relatively great amount of muscular activity. On the other hand, as is well known from study of other animals, the internal processes of the organism may of themselves be greatly stimulated by the presence of food in the alimentary tract. Basal metabolism as commonly measured is that metabolism obtaining when the animal is in complete muscular repose and in the post-absorptive condition, that is, after active digestion has ceased. It has already been emphasized that with the elephant it is practically impossible to secure both of these conditions.

With most animals the condition of complete muscular repose is obtained when they are lying down and quiet. When the elephant lies down, it does so only for a short time. When the elephant is standing, there is apparently a great deal of physical activity, but careful analysis shows that this is more apparent than real. (See page 66.) As a result of extensive experience with large ruminants in stalls inside of a respiration chamber, it is believed that the stall activity of the elephant is perfectly comparable to that of the cow, bull, or steer, and in all probability the metabolism would not be significantly increased by stall activity unless the animal was distinctly unruly. An animal when lying produces less heat than when standing. It has been found that the larger ruminants, the horse, and other animals have a metabolism approximately 10 per cent higher when standing in a stall than when lying.[1] With some animals, particularly the quadrupeds, the difference in metabolism with difference in body position is believed to be a little less than this. The fact that the horse frequently sleeps while standing makes it directly comparable to the elephant, which not infrequently dozes in this position. In the case of the horse it has been found that the action current (the electric current set up in a muscle by its tonus when called upon to do work) of the hind legs is at a minimum when the horse is standing. This indicates that, with the horse, standing is accompanied by little muscular exertion. It is reasonable to suppose that the economy in standing is the same with the elephant as with the horse, if not greater. This belief is based upon observations on the heart rates of the elephants in the Ringling herd in Florida, where the heart rates were found to be somewhat higher when the elephants were lying than when standing. This suggests that the activity incidental to maintaining the standing position is not considerable, a supposition in full conformity with the conclusion drawn from the study of the horse. Consequently it is argued that a reduction of 10 per cent in metabolism measurements made on an elephant while standing, to approximate the metabolism of that animal while lying, is fully on the side of being too large rather than too small.

The correction to be made to attempt to have the metabolism measurements on the elephant correspond to those that would have been obtained in the post-absorptive state is a problem of a very different order, demanding consideration of the influence of the ingestion of food. Invariably the ingestion of food results in an increase in metabolism. The amount of increase can be predicted with great accuracy for humans because of the many studies made. With humans the increase in metabolism is largely associated with ingestion of protein, although ketose sugars likewise stimulate the metabolism highly. With Carnivora and Omnivora also the stimulus is associated with ingestion of protein. The situation with Herbivora, however, is different. These animals subsist chiefly upon carbohydrates and yet, as has been shown at the Agricultural Experiment Station at Durham, New Hampshire, by Professor E. G. Ritzman, the metabolism of the non-lactating cow on a maintenance hay ration may be stimulated by the ingestion of food to 50 per cent above the basal metabolism determined on the fourth and fifth days of fasting, and that of a lactating cow on super-maintenance rations may be increased 100 per cent or more.

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[1] This increase due to stall activity is strikingly lower than the increase of 40 per cent or more in the metabolism of birds when active (without actually flying) inside a respiration chamber. See Benedict, F. G., and E. L. Fox, Arch. f. d. ges. Physiol., 1933, 232, p. 366.

The exact cause of the increase in metabolism due to the ingestion of food is not known. Originally it was thought that the mechanical work of handling this large ballast in the intestinal tract accounted for the increase. This view, however, is held by only a relatively few extremists, for innumerable experiments on humans and other animals have shown that the purely mechanical factor can play but a very small rôle. The fermentation factor plays a rôle in the metabolism of Herbivora, particularly ruminants, far greater than it does with dogs and with man. The prolonged stay in the intestinal tract of large masses of easily fermentable carbohydrate material at a body temperature of 37° C. (ideal for the development of bacteria and for the enzyme actions) gives rise to the development of extensive fermentations accompanied by the production of methane and carbon dioxide. In the case of the elephant the production of methane may amount to 655 liters in 24 hours. The actual amount of extra heat produced during the processes of fermentation is believed to be small, based upon experiments *in vitro,* and the mere disengagement of methane and carbon dioxide with an accompanying small amount of heat production can play no significant rôle with the elephant. On the other hand, it has been conclusively demonstrated that among the stimuli to increased heat production as the result of taking food no factor with Herbivora, particularly ruminants, is greater than the products of fermentation, chiefly organic acids. Only by this type of hypothesis[1] can one explain why it is that the carbohydrate material, such as that eaten almost exclusively by the elephant and the larger domestic animals, should stimulate the metabolism of these animals so enormously.

When food is denied Herbivora, or ruminants, there are two simultaneously appearing effects—a rapid cessation in the formation of methane and concomitantly a rapid decrease in the animal's metabolism. Hence it is logical to assume that these two factors are intimately associated. If in the same animal, for example a steer or a cow, there is a close association between the quantity of the products of fermentation and the internal heat production, or metabolism, it is reasonable to assume that with animals of different species the degree of metabolic stimulus resulting from the ingestion of food may be approximately proportional to the intensity of the fermentation processes. This assumption rests upon two other premises, namely, that the methane is the true and only measure of the fermentative processes and that the concomitant fermentation products (chiefly organic acids, that is, commonly associated with, if not productive of, the stimulus to metabolism) are proportional to the methane production. Frankly, these assumptions are seriously to be challenged, owing to the distinct differences in the nature of the digestive processes of certain of the different species of animals. However, the assumptions have, for purposes of argument, been made in the case of the elephant and the cow. With these animals measurements are available of the methane production. As has already been pointed out (see page 258), the methane production of the non-lactating cow on maintenance hay rations may be 7 or 8 per cent of the volume of carbon dioxide produced, and the basal heat production may be increased 50 per cent by the accompanying products of fermentation, not by the methane production itself or the carbon dioxide accompanying the production of methane but probably by the products of fermentation. With the elephant the fermentation factors are less pronounced, in part due to the shorter length of time that the food remains in the alimentary tract, and particularly due to the poorer comminution of food, and the methane production averages only 4 per cent of the carbon-dioxide output, a relationship half as great as that noted with the cow. It may, therefore, be argued that the stimulus due to food would be half as great with the elephant as with the cow, *i. e.,* 25 per cent.

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[1] Grouven, H., *Physiologisch-chemische Futterungsversuche. Zweiter Bericht über die Arbeiten der agrikulturchemischen Versuchsstation zu Salzmunde,* Berlin, 1864, p. 505.

If to the 25 per cent assumed to be the stimulus of digestive activity is added the 10 per cent correction for the influence of standing, this would mean that the elephant's standard metabolism (standing and in digestive activity) should be reduced by 35 per cent to bring it to the basal level. That the digestibility of the elephant is very poor and that the food passes through the intestinal tract relatively rapidly lead to the conviction that this correction of 35 per cent is somewhat too high. Hence it is arbitrarily assumed that the corrections for standing and digestive activity would be together more nearly of the order of 25 per cent rather than 35 per cent. The purely mechanical factor of the transport of food material through the intestinal tract has been neglected in this assumption of 25 per cent. Since Jap had as much as 50 kg. of hay per day, the neglect of this factor may be challenged. However, 50 kg. of hay for an animal weighing approximately 4000 kg. represents only about 12 grams for an animal of 1 kg. The amount of food eaten by Jap was, therefore, in proportion to her weight, much less than that ordinarily eaten by the cow and the steer, and it is commonly believed that the mechanical factor of transport of food plays an insignificant rôle in the metabolism of the cow and the steer.

The above method of estimating the probable effects of standing and digestive activity is far from being as satisfactory as would be the direct measurement of the elephant in the post-absorptive condition. As has already been discussed (see page 240), Brody in correcting his metabolism measurements on the elephant in trunk-breathing experiments has made a rough estimate that the increase in metabolism due to standing would be 10 per cent and that due to food, 20 per cent, totaling 30 per cent. This correction is 5 per cent higher than the correction of 25 per cent decided upon in the above analysis. On the assumption that the correction factor of 25 per cent is not too far from exact, Jap's basal metabolism has been calculated as follows.

TOTAL BASAL HEAT PRODUCTION

As has been explained on pages 267 and 268, the average standard metabolism of Jap, standing and with digestive activity, has been calculated to be 64,800 calories per 24 hours. If a reduction of 10 per cent is made in this value to correct for the influence of standing and a reduction of 15 per cent to correct for the effect of digestive activity, *the probable basal metabolism of Jap, lying and post-absorptive, thus becomes 49,000 calories per 24 hours.*

From the practical standpoint, for the establishment of the energy balance and for the establishment of the energy requirements of the elephant per 24 hours, neither of these assumptions is necessary, as one is interested in knowing the ordinary 24-hour energy needs irrespective of whether the animal is standing or lying and irrespective of whether it is in the digestive state or not. If an elephant is to be fed to meet the energy needs for stall activity while in winter quarters, that is one thing; if an elephant is to be fed to meet the energy needs not only of stall activity but the superimposed needs of severe muscular work, such as that engaged in by the Barnes herd, this is an entirely different problem. The actual measurement of the metabolism of the elephant during severe muscular work presents engineering problems that probably never will be satisfactorily solved. From the standpoint of pure physiology, however, it is important to approximate as closely as possible the true basal metabolism of this largest terrestrial mammal. For this reason the attempt has been made to correct for the factors of muscular and digestive activity. The respiration experiments on Jap are not completely satisfactory. They could be bettered extensively, even by repetition with precisely the same technique. Thus, the determination of the food intake should be studied over a much longer period than was done and should cover a period simultaneous with the respiration experiments. The respiration experiments should be extended to include, if possible, measurements when the animal is lying and particularly when it is sleeping. It is doubtful whether an elephant can be found that will submit to fasting for any length of time. Collections of urine should be made for 24-hour periods, simultaneous with respiration experiments, with a well-trained elephant having a keeper fully *en rapport* with it. However, the effect of the stimulus of digestion will always remain an uncertain factor. Without experiments in the incipient stages of fasting, this effect can not be directly determined. The Nutrition Laboratory's experience with other fasting animals and its experience in digestion experiments with ruminants, however, lead to the belief that the above method of reasoning and the treatment of the data obtained on this elephant indicating 49,000 calories as her most probable basal metabolism are as accurate as possible at the present day.

COMPARISON OF THE BASAL METABOLISM OF THE ELEPHANT WITH THE BASAL MEASUREMENTS ON OTHER ANIMALS

Basal Heat Production Per Kilogram of Body Weight

Since the elephant is such a large animal, one is not surprised that its calculated total basal heat production is 49,000 calories. This fact by itself, however, is not of particular significance; it is of more interest to compare the elephant's metabolism with that of other animals, to establish whether the elephant has a relatively high or a relatively low metabolism. The problem of comparing directly metabolism measurements on one animal species with those on another has been confronting physiologists for over half a century. The difficulties encountered in ruling out the effects of physical and digestive activity, the standing position, and sleep have already been touched upon. With man, dogs, and many other animals, it is usually possible to secure the greatest degree of muscular repose and the post-absorptive condition. Since the metabolism is somewhat lower during sleep than during the waking condition, experiments during sleep are often attempted, although this introduces an element of uncertainty, since it is impossible to insure measurements during sleep with all animals. Furthermore, the metabolism of the sleeping, quiet rabbit or mouse can not be compared directly with the metabolism of the nervous, restless horse. However, basal metabolism measurements as ordinarily made do succeed in ruling out in large degree the effects of these various factors, and for the elephant an arbitrary correction has been made in the attempt to eliminate such effects.

There remains a further difficulty to be considered in any intelligent comparison of basal metabolism measurements on different species of animals. The elephant occupies a peculiar position among the animals that the Nutrition Laboratory has studied, inasmuch as it is by far the largest terrestrial mammal (several times the size of the largest steer or horse) that has ever been studied in respiration experiments. Does size *per se* introduce any special factor in the basal metabolism of these enormous animals that is not seemingly introduced in a proportionate degree with smaller animals?

When animals of different species of the same weight are to be compared, there is no special problem in size itself. But when animals vary greatly in body size, direct comparison is impossible. One of the earliest methods of making comparisons in such cases was on the basis of body weight, on the assumption that a 10-kg. animal would have a much lower total heat production than a 1000-kg. animal. To put the metabolism measurements on these animals on a comparable basis, they were expressed in terms of the heat production per kilogram of body weight. This comparison, however, tacitly assumed that the heat productions of given masses of weight, irrespective of size, are comparable. It was early noticed that this is by no means the case, and that the heat production per unit of body weight is always much greater with small animals than with large animals.

Thus, specifically, the basal heat production of a 20-gram mouse is about 170 calories per kilogram of body weight per 24 hours, whereas the basal heat production of a 64-kg. man would be more nearly 25 calories per unit of weight. The basal metabolism of a 600-kg. Percheron mare has been found to be 22 calories per kilogram of body weight and that of a 500- or 600-kg. cow or steer about 15 calories. The basal metabolism of the elephant Jap, weighing 3672 kg., has been calculated to be 13 calories per kilogram of body weight. It is thus seen that, although the elephant (an animal of huge size) has a *total* heat production larger than that of any other animal that has ever been measured, nevertheless per kilogram of body weight its metabolism is lower than that of the other animals.

This comparison, which supports the early finding that larger animals have a lower heat production per unit of weight than smaller animals, also suggests that there may be a limiting size beyond which this rule is not applicable, that is, that once this limiting size is attained or exceeded by any species of animal, the difference in metabolism with respect to size will practically disappear. Thus, the Nutrition Laboratory series of observations on different animals shows that animals ranging in size from the 50-kg. sheep to the 500- or 600-kg. steer and cow all have a basal heat production ranging only from about 28 to 15 calories per kilogram and averaging close to 22 calories, with the 600-kg. steer producing about 15 calories. The elephant, weighing eight times as much as the cow and the steer, has a probable basal heat production per unit of weight only about 10 per cent lower than that of these animals, that is, in no sense in direct proportion to the difference in body weight. The large changes in the heat production per kilogram of body weight noted with the small animals weighing from 20 grams to 50 kg. in large part disappear beyond the weight of 50 kg. It is, therefore, a question whether the curve for the relationship between the size and the basal heat production per unit of weight may not definitely flatten out at weights of about 500 kg. and remain at a reasonably constant level thereafter. In such comparisons as this it is especially regretted that there are not metabolism measurements on more elephants and that the measurements on Jap were not made under more sharply determined basal conditions. Judging from all the other factors that have enabled a comparison of Jap with other animals (a comparison showing the complete normality of Jap), one could logically assume that her metabolism is representative of elephants as a whole and consequently that the value of 13 calories per kilogram may be accepted as a measure of the basal metabolism of a 4000-kg. elephant.

Basal Heat Production Per Square Meter of Body Surface

Although the heat production per kilogram of body weight, as has been seen, is far from constant with animals of different sizes, investigators have been trying for decades to establish some correlation between the size of the animal and its heat production. A most logical and a distinctly alluring hypothesis was based on the assumption that, since the total heat production of an animal is equal to the heat loss, the heat loss is determined by two factors, (1) the difference in potential between the temperature of the environment and the temperature of the animal and (2) the area of the animal's body exposed to heat loss. Thus the heat production was supposed to reflect an apparently close relationship between the surface area and the heat loss. This relationship was brought to a presumably accurate physiological basis by Rubner,[1] who, in enunciating his "law of surface area," stated that all warm-blooded animals have the same heat production per square meter of body surface per 24 hours. The experimental data used by Rubner for establishing this "law" consisted chiefly of a series of experiments on dogs varying in size from 3 to 31 kg. These showed a remarkably uniform heat production of about 1000 calories per square meter per 24 hours. Subsequently measurements on other species of animals led E. Voit [2] to the conviction that this holds true for animals in general. In his last analysis of the situation, however, Rubner pointed out that many investigators have not recognized the differences that existed in the conditions under which the earlier tests were made for comparative purposes, namely, differences in length of time after food, differences in activity, and particularly differences in the temperature of the environment.[3] Rubner had worked at a laboratory temperature of 16° C. This was a convenient temperature at which to make measurements, and all his dogs were studied at this temperature. But animals were soon found to show striking differences in metabolism depending upon whether they were measured at high or low temperatures. It then became apparent that with most animals the minimum metabolism occurs at temperatures near 28° C., that is, 12 degrees higher than the temperature at which Rubner made his experiments. These finer points, however, are rarely considered by writers on metabolism, and the old statement by Rubner that the basal metabolism of all warm-blooded animals is approximately uniform at 1000 calories per square meter of body surface is commonly quoted, without any refinements.

The Nutrition Laboratory has been engaged for decades in studying the metabolism of animals of different species under two conditions, (1) at 16° C. and (2) to note that environmental temperature at which the minimum metabolism is found, usually 28° C. Ideally it would have been preferable if Jap could have been measured under conditions best suited for comparative purposes, conditions inferred from Rubner's earlier statements and demonstrated from subsequent experience, namely, in complete muscular repose, lying, in the post-absorptive condition, that is, after the period of active digestion has ceased, and at that environmental temperature at which the metabolism would be minimum (for most animals not far from 28° C.). Furthermore, to make the data more strictly applicable to a study of Rubner's law of surface area, measurements at or near 16° C. would also have been ideal. With the time available it was impracticable to meet all these requirements, important though they are. The metabolism measurements on Jap were, therefore, confined to environmental temperatures between 20° and 25° C. There is no proof that the minimum metabolism of the elephant prevails at these temperatures. It is highly probable, however, that these temperatures had no pronounced effect; in other words, that the zone of thermic neutrality for the elephant is rather wide. On one day the respiration chamber temperature reached nearly 25° C., that is, it approached the commonly accepted temperature for minimum metabolism

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[1] Rubner, M., Zeitschr. f. Biol., 1883, **19**, p. 535.

[2] Voit, E., Zeitschr. f. Biol., 1901, **41**, p. 113.

[3] Rubner, M., Sitzgsber. preuss. Akad. Wiss., Physik.-math. Kl., 1931, **17**, p. 272.

(28° C.). On this particular day the heat production of Jap was the highest, suggesting that at 25° she was really uncomfortably warm, a condition usually met with in other animals only when the environmental temperature is somewhat over 30° C. This analysis suggests, however, that under the conditions of measurement Jap's metabolism was measured well within the zone of thermic neutrality, although animals without fur are usually expected to have a narrower zone of thermic neutrality than those well furred.

Since the measurements with Jap were made only between 20° and 25° C., any comparisons of her metabolism with that of other animals must take into account the differences that may exist in measurements at temperatures above or below 28° C. The evidence is in favor, however, of the view that Jap's metabolism was essentially minimum, so far as environmental temperature was concerned. This is believed to be particularly true of this animal, because she had shown an extraordinary resistance to cold. Her adaptation to low temperatures, even as low as 0° C., was astonishing, and it is probable that by long experience she had so adjusted her basal heat production that an environmental temperature of 25° C. did not affect it.

Calculation of the surface area of the elephant—At first sight it would seem to be relatively simple to determine the surface area of the elephant by any one of the commonly known methods, particularly the surface integrator method used by Brody or some method of triangulation. Because of the pressure of other observations at the time, this measurement was not made. This omission was justified by the belief of the Nutrition Laboratory that the formula $S = 10 \text{ x } w^{\frac{2}{3}}$ will give very closely the surface area of any animal. Careful analysis [1] of all the existing measurements of body surface on animals of greatly different configurations has shown that there may be deviations of ± 10 per cent in the factor of 10 in this formula. This constant for an animal of the configuration of Jap probably is low rather than high. It is doubtful if it would be as low as that recommended for the fat steer (8.4) but it might be somewhat under 10. Furthermore, if one were to attempt to correct the body weight for weight of intestinal contents (see page 106), this would result in a still lower surface area. In other words, if there is an error in calculating the surface area of the elephant from the formula $S = 10 \text{ x } w^{\frac{2}{3}}$ (in which w equals the *total* body weight in grams), it is in the direction of furnishing an area somewhat larger than the true area. Since the elephant remains standing practically the entire twenty-four hours and, even when lying, stretches out its limbs fairly well, it is doubtful if many animals would present relatively as large a proportion of surface area for heat loss as does the elephant. The dog and the cat, when lying, would curl up. The lying position of the horse and other animals tends to restrict considerably the exposure of the surface and to result in large amounts of protected area, such as the axilla and the groin. With the elephant this reduction in exposed surface is probably less than with any other animal. Those who are inclined, therefore, to lay special emphasis upon the surface area as a factor in the loss of heat must not overlook this point. Calculation of Jap's body surface by the formula $S = 10 \text{ x } w^{\frac{2}{3}}$ certainly may be considered as accurate as the measurement of the standard metabolism and the calculation of the probable basal metabolism. On this basis, Jap's surface area would be 23.8 square meters.

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[1] Benedict, F. G., Asher-Spiro's Ergebnisse d. Physiol., 1934, **36**, p. 300.

Since the total basal heat production of Jap per 24 hours has been calculated to be 49,000 calories, and from the above formula the surface area is 23.8 square meters, *it follows that the basal metabolism per unit of surface area is 2060 calories.* This value can not be appreciably lowered, even if allowances are made for possible differences in the factors used to calculate the surface area and to correct for the effects of standing and digestion. This value of 2060 calories is twice as great as the classic figure of 1000 calories reported by Rubner [1] and confirmed by Voit.[2] Rubner,[3] however, has pointed out that the value of 1000 calories was determined at 16°, and that if the measurements were made at thermic neutrality (30° C.), the value would be nearer 600 calories. As already stated, it is believed that Jap was measured at very nearly thermic neutrality. Hence if 600 calories is accepted as the probable basal metabolism of smaller warm-blooded animals at thermic neutrality, the elephant's metabolism is at least three times that. This comparison serves to show the inadequacy of the surface area conception when applied to animals ranging in size from those as small as mice to those as large as elephants.

It is thus seen that the elephant has the highest heat production per square meter of surface area of any of the animals thus far studied. A natural inference would be that this is explained wholly by the fact that the elephant is a hairless animal and that other hairless species, such as the hairless mouse,[4] have been shown to have a higher metabolism than the well-furred animals. It is believed, however, that this explanation does not hold true, for the elephant (so far as we know) has a wide zone of thermic neutrality, whereas the hairless mouse has a very narrow zone and a very high critical temperature. Secondly, it is believed that the heat production of the elephant is large per square meter of surface area because it is a large animal with a high total heat production and a relatively small surface area. It has already been demonstrated that large domestic animals like the ox and the horse have a heat production per square meter of surface area far above the 1000 calories commonly ascribed to them. By this method of comparison, therefore, the elephant has a metabolism per square meter of surface area sensibly higher than that of any other mammal thus far studied.

SPECULATIONS REGARDING THE BASAL METABOLISM OF THE ELEPHANT AND OF THE WHALE

The importance of comparing the metabolism of the elephant with that of other animals has already been touched upon. This comparison has dealt particularly with animals much smaller than the elephant, as the animal nearest in size to the elephant the metabolism of which has been studied is the Percheron horse, having a body weight only about one-seventh that of the elephant. Furthermore, the largest animals next in size to the elephant, namely, the horse, the cow, and the steer, are all reasonably well protected with hair, whereas the elephant is a hairless animal. Both, therefore, by virtue of size and by virtue of the nature of the protective covering, one may well expect differences in the heat loss and consequently in the heat production of these several animals. The comparison of the metabolism of animals of various sizes has long been made, frequently, however, without attention to the necessity in such comparisons of having the measurements made under identical conditions. Until such conditions are adhered to, obviously measurements made on different animals in different laboratories can not be summarized and used for logical interspecific comparisons of basal metabolism. For such comparisons an extensive series of experiments under strictly comparable conditions alone can be used. To this end the Nutrition Laboratory has, during the past three decades, been accumulating basal metabolism data on a large number of different species of animals. In due time these will be given careful analysis to determine, if possible, whether the measurements of heat production are related in any special way to the various physiological groups and the various sizes of animals studied. At the present time the only clear evidence is what has long been known, namely, that the heat production per kilogram of body weight is in general larger the smaller the animal, and that the heat production per square meter of body surface is by no means so constant as it was formerly thought to be. A variation of at least 400 per cent in the metabolism as expressed on this latter basis has been found in the Nutrition Laboratory's own data for the smallest (mouse) and the largest (elephant) mammals.

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[1] Rubner, M., Zeitschr. f. Biol., 1883, **19**, p. 535.
[2] Voit, E., Zeitschr. f. Biol., 1901, **41**, p. 113.
[3] Rubner, M., Sitzgsber. preuss. Akad. Wiss., Physik.-math. Kl., 1931, **17**, p. 313.
[4] Benedict, F. G., and E. L. Fox, Arch. f. d. ges. Physiol., 1933, **231**, p. 455.

At the present time the elephant has the largest weight of any animal thus far studied, the lowest heat production per kilogram of body weight, and the highest heat production per square meter of surface area. The importance of knowledge regarding the metabolism of large mammals has been emphasized by a number of writers, but purely in a speculative way, for until the measurements on Jap no positive information was at hand for the elephant and there are still no direct measurements on the largest living mammal, the whale. In 1918 Pütter [1] calculated that the oxygen consumption of an elephant having a weight of 3500 kg. would be, based upon its estimated food consumption, about 12 or 15 liters per minute under stall conditions of feeding, values from 20 to 50 per cent higher than the measured oxygen consumption of Jap of 10 liters, which was also obtained under feeding conditions. In comparisons of the calculated metabolism of animals of different sizes, Pütter points out that the oxygen consumption per unit of body surface increases with the size of the animal and that it is probably even larger with the whale than with the elephant. He concludes that the body surface law does not hold for animals of such large size. Subsequently, in 1923, Pütter [2] published further considerations regarding the probable metabolism of the whale.

Theoretical speculations with regard to the basal metabolism of the elephant and that of the largest living mammal, the whale, were engaged in by Rubner in 1924.[3] He inferred that the heat production of the elephant per unit of weight might actually be lower than that of a cold-blooded animal like the fish, and for this reason emphasized that there can be no sharp differentiation between cold-blooded and warm-blooded animals. Jap's basal metabolism at thermic neutrality has been calculated to be 13 calories per kilogram of body weight. Rubner calculates that the goldfish at 16° C. has essentially this same heat production. Subsequent study of the metabolism of cold-blooded animals, however, based upon the experiments made by the Nutrition Laboratory[1] on large cold-blooded animals and upon the extraordinarily careful work of Krogh[2] on smaller animals, including fish, shows that at 16° C. Krogh's goldfish, weighing 9 grams, had a heat production of 8 calories per kilogram.

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[1] Pütter, A., Arch. f. d. ges. Physiol., 1918, **172**, p. 367.

[2] Pütter, A., Zool. Jahrb., Abt. f. allg. Zool. u. Physiol., 1923, **40**, p. 217.

[3] Rubner, M., Biochem. Zeitschr., 1924, **148**, p. 240.

Rubner calculates that with a whale weighing 150,000 kg. the 24-hour basal heat production may not rise above 1.7 calories per kilogram of body weight at normal blood temperature. The general trend of the values for the heat production per unit of weight with various animals, however, does not suggest a decrease with increasing weight to anywhere near this low level.

A particularly interesting discussion of the probable basal metabolism of the whale is given by Barcroft,[3] who, dealing with the problem of alleged prolonged submergence, propounds the question as to how long 1700 liters of oxygen might be expected to last a whale. Barcroft cites the following data given to him by Laurie,[4] a member of the *Discovery* Expedition to South Georgia.

"The subject observed was a blue whale. The observations were made at Stromness.

Length	27 m.
Weight	122,004 kg.
Approx. weight of muscle	56,444 kg.
Blood volume (expressed in kg. but probably measured in liters)	8,000 kg.
Heart	631 kg.
Average oxygen capacity of 17 other whales	213 cc. per liter
Taking the oxygen capacity at 213 cc. 0_2 per liter of blood, that of the blood of the Stromness whale would be approximately	1,700 liters"

Barcroft lays particular stress upon the fact that the oxygen consumption would be proportional to the muscles, which in this instance weighed 56,444 kg. In spite of his conservative remark, however, that "It can not be stated too clearly that we have no real knowledge as to whether the whale falls into the calculated place which would assign to it a metabolism per kg. of only one-tenth that of man," he does subsequently assume a consumption of 20 liters of oxygen per minute as the basal metabolism of the whale. This whale weighed 122,004 kg., a weight obtained under great difficulties but probably not far from correct.

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[1] Benedict, F. G., Carnegie Inst. Wash. Pub. No. 425, 1932, p. 455.

[2] Krogh, A., Internat. Zeitschr. f. physik.-chem. Biol., 1914, **1**, p. 491; Ege, R., and A. Krogh, Internat. Revue f. Hydrobiol., 1914, **6**, p. 48.

[3] Barcroft, J., *Features in the architecture of physiological function,* Cambridge, 1934, p. 121.

[4] Laurie, A. H., *Some aspects of respiration in blue and fin whales, Discovery* Reports, 1933, *7*, p. 363.

The measured oxygen consumption of Jap was 10 liters per minute. On the assumption that the correction for the influence of standing and digestive activity would amount to 25 per cent, Jap's basal oxygen consumption would be approximately 7 liters per minute. Thus to the whale, weighing more than twenty-five times as much as Jap, Barcroft ascribes a total oxygen consumption of but three times that of Jap.

Laurie himself, calculating that the surface area of this Stromness whale (according to the method of Guldberg [1]) was 275 square meters and accepting the old legend of 1000 calories per square meter of body surface, estimates that the whale's basal metabolism would be 275,000 total calories per day or 2.25 calories per kilogram of body weight per day. On the basis that the whale's basal metabolism per kilogram is 14.6 times less than that of a 70-kg. man having an oxygen consumption of 4.28 cc. per kilogram of body weight per minute, Laurie concludes that the whale would require 35.75 liters of oxygen per minute, an estimate even higher than that made by Barcroft and five times the oxygen consumption of the elephant Jap.

Krogh [2] points out that it might be possible "to arrive at a value for the metabolism by calculating the heat loss from an internal temperature of 35° C., a water temperature of, say, 5° C., measurements of the thickness of blubber and its properties as a conductor of heat." But he apparently accepts Laurie's calculation of the surface area of the whale and does not question the assumption of 1000 calories as the heat production per square meter of body surface, for he makes use of Laurie's estimate of the metabolism under conditions of rest to calculate the metabolism of the swimming whale.

These comparisons serve to stress the debatability of making these speculative calculations and the importance of knowing as accurately as possible the basal metabolism of the largest warm-blooded animals that are available for measurement. They likewise emphasize the conclusion expressed by Barcroft that real knowledge regarding the whale is not at hand. A significant paragraph in Barcroft's book which, although referring specifically to the whale, applies with equal force to the elephant, is as follows:

> "The intensity of the normal metabolism of the whale appears to be perhaps the most compelling problem in the, as yet, unascertained knowledge of the whale physiology. If that intensity were known, probably many other problems would be solved automatically."

Obviously the heat production of the whale can never be measured, and only when metabolism measurements have been made on all the other species of animals and the relationships established for these animals, will one be able to predict with a reasonable degree of accuracy the probable metabolism of the whale. Although it will be difficult to secure a quieter, more cooperative elephant than Jap, and hence our findings are in a high degree representative of a quiet elephant, the need for confirmation on other elephants is obvious when one sees what important zoological and physiological facts are involved in a study of this sort.

[1] Guldberg, G., *Ueber das Verfahren bei Berechnung des Rauminhaltes und Gewichtes der grossen Waltiere,* Forhandlinger Videnskabs-Selskabs, Christiania, 1907, No. 3.

[2] Krogh, A., Nature, 1934, 133, p. 635.

SALIENT FACTS REGARDING THE PHYSIOLOGY OF THE ELEPHANT

At the request of practical elephant men and zoological park officials who have known of the preparation of this book, the following data are abstracted from the text for ready reference. In many instances it is difficult to give one line of text, much less a single figure, to cover an extensive study. Yet, for purely practical purposes, this has been attempted. Following each statement is indicated the page of the book where the particular topic is discussed in detail. In many instances the statements are based upon observations made on several elephants, usually a total of sixty-three Indian elephants (all females, except one). In other instances they are based upon observations upon only one elephant, named Jap (female). These latter instances are indicated by the word "Jap" in parentheses following the italicized side head. For practical purposes, many figures reported are expressed both in the English and the metric system.

Age—The extreme ages attributed to elephants are not true. The elephant has about the length of life of man. An elephant of 80 years is an old animal. (Page 62.) The average age of the circus elephant is about 33 years.

Muscular activity—Although the elephant is seemingly incessantly active, only the smaller parts of the body (tip of trunk, ears, and tail) are extensively moved. The body as a whole is relatively quiet, except during "weaving." (Page 64.)

Sleep—Many elephants doze standing up, but under favorable conditions they will lie down to sleep, particularly between 11 p.m. and 4 a.m. They remain lying for a relatively short time, standing up frequently to urinate or defecate. (Page 68.)

Temperament—Although for the most part docile and tractable, elephants are subject on the slightest provocation to excitation and alarm. (Page 75.)

Sexual maturity—Probably as early as 10 to 12 years of age. (Page 77.)

Rut—Very irregularly noticed and not pronounced with most females. More pronounced in the males. Flow of the temporal glands apparently not correlated with rut, although marked flow usually appears with rut. (Page 78.)

Period of gestation—From 18 to 22 months, probably 20 months. Newborn babies weigh from 170 to 250 pounds (77 to 113 kg.) or 3 or 4 per cent of the mother's weight, and are about 3 feet (91 cm.) tall at the shoulder. (Pages 81 and 84.)

Weight—A "large" elephant weighs over 8000 pounds (3630 kg.). The average circus elephant weighs 6000 pounds (2720 kg.), ranging from 2300 to 9200 pounds (1040 to 4170 kg.). (Table 2, page 22.)

Intestinal contents represent about 10 per cent of the total body weight, that is, much less than noted with large ruminants. (Page 106.)

Weight of heart—Autopsies of elephants indicate that the heart weight is equal to about one-half of one per cent of the total body weight. (Page 135.)

Height—A simple device is described for accurate measurement of the height of the elephant at the shoulder. Twice the circumference of the right front foot does not indicate accurately the true shoulder height of the elephant. (Page 95.) A simple, reasonably accurate method is to throw a tape over the shoulder at the highest point and measure from the outside of the right to the outside of the left foot. From half this length should be subtracted 8 inches. (Page 100.) Elephants over 8 feet at the shoulder are *very tall.* The tallest actually measured by us was 8 feet 2 inches (2.49 meters). The average height of the circus elephant is 7 feet 4 inches (2.24 meters). (Pages 22 and 93.)

Respiration rate—Standing and awake, about 10 per minute; lying quietly, from 4 to 5 per minute. (Page 114.)

Ventilation of lungs (Jap, 8095 pounds or 3672 kg.)—May amount to 310 liters (10.9 cubic feet) per minute, at standard conditions of temperature and pressure. (Page 120.)

Heart rate—Standing, 28 beats per minute; lying, 35 beats per minute. (Page 122.)

Body temperature—Temperature of the urine, 35.9° C. (96.6° F.). (Page 139.) Temperature of the feces is 0.7° C. (1.3° F.) higher. (Page 146.) The body temperature may be rapidly determined by inserting an ordinary mercurial thermometer in a ball of feces. The temperature read on this thermometer should be reduced 0.7° C. or 1.3° F. (Page 149.) Temperature of air expired from tip of trunk, 31° C. (88° F.) (Page 150.) Skin temperature, depending upon the air temperature, from 26° to 30° C. (79° to 86° F.) (Page 153.)

Food—In the United States elephants are fed mostly hay, supplemented by bran and oats. A large elephant eats about 150 pounds of hay per day. (Page 159.)

Water—A full-grown elephant will drink about 50 gallons (189 liters) of water per day, preferably at a warm temperature. (Page 173.) The elephant can take into its trunk about 5 liters or 1½ gallons of water at one time. (Page 174.)

Feces—Five or six large boluses are passed at one time. These may weigh as much as 2 kg. (4½ lbs.) each. Defecations about 14 to 18 per day. Total daily amount is 110 kg. (240 lbs.) Chemical composition of feces is much like that of poor hay. (Page 176.)

Rate of passage of food through intestines—About 24 hours. (Page 189.)

Apparent digestibility of hay—Extremely poor. Only about 44 per cent of the dry matter and also of the energy content is digested, as compared with 50 to 70 per cent with the cow, steer, sheep, and horse. (Pages 192 and 195.)

Urine characteristics—Slightly more frequent passing at night and following the drinking of water. (Page 200.) Straw-colored, no pronounced odor, usually turbid rather than clear. (Page 201.) Reaction is, on the whole, acid. Microscopy shows no pathological findings. Frequent calcium oxalate crystals. (Page 201.) Specific gravity, on the average, is 1.019; range from 1.004 to 1.033. (Page 204.)

Volume of urine discharged (Jap)—A single discharge amounts, on the average, to 5 liters (1½ gallons), and the maximum individual discharge may be 10 or 11 liters. (Page 203.) The total volume discharged per day is calculated to be 50 liters (15 gallons). (Page 203.)

Total solids in urine (Jap)—A large elephant excretes over 2 kg. (4½ lbs.) of total solids in the urine per day, of which one-fifth is mineral and four-fifths organic matter. (Page 209.)

Urinary nitrogen excretion—About 5 milligrams of nitrogen per cubic centimeter of urine are passed. (Page 214.) The total 24-hour excretion of nitrogen by the elephant Jap (3672 kg.) was 235 grams. (Page 216.)

Partition of urinary nitrogen excretion (Jap)—The high percentage of total nitrogen in the form of urea, the low percentage of ammonia-nitrogen, and the low creatinine coefficient indicate that the elephant has an extremely low endogenous metabolism. Elephant's urine contains detectable amounts of hippuric acid. (Page 220.)

Sodium-chloride excretion (Jap)—About 160 grams (5½ ounces) of sodium chloride (common salt) are excreted in the urine per day. (Page 230.)

Carbon and energy in urine—The urine contains from 5 to 20 milligrams of carbon per cubic centimeter, depending upon the feed, and may have an energy value varying from 65 to 200 calories per liter. For each gram of total solids 0.3 gram of carbon may be expected. Each gram of carbon in urine has an energy value of 10 calories, each gram of total solids 3.2 calories, and each gram of organic matter 4 calories. (Page 225.)

Energy and nitrogen balance (Jap)—With a daily food intake of 50 kg. (110 lbs.) of hay, Jap had a slight excess of calories and of nitrogen. (Pages 228 and 271.)

Trunk-breathing experiments (Jap) with a mask on the trunk give values about 30 per cent too low (due to losses through the mouth) for the respiratory products (carbon dioxide and oxygen). (Page 267.)

Methane (Jap)—In the air from the trunk one finds methane, a product of intestinal fermentation, in the proportion of about one volume of methane for every one hundred volumes of carbon dioxide eliminated. (Page 245.) Respiration chamber experiments showed that one-fourth of the total methane excretion may be eliminated through the trunk and the mouth and three-fourths through the anus. (Page 256.) For every one hundred volumes of carbon dioxide eliminated there was a *total* discharge of four volumes of methane. (Page 258.)

Water-vapor output (Jap)—There were 22 kg. (48 lbs.) of water vaporized per day from both the lungs and the skin. Of this about 50 per cent was from the skin. About 20 per cent of the total heat given off was lost in the vaporization of water. (Page 273.)

Heat production (Jap)—The total heat production of Jap (3672 kg.) while standing, on feed, and at a barn temperature of 20° C., was 65,000 calories per 24 hours. (Page 267.) It is calculated that this total heat production should be reduced 25 per cent, to correct for the increase due to the effort of standing as compared to lying, and for the increase due to the eating of food. (Page 280.) Hence the total basal (lying, with no digestive activity) metabolism of Jap was 49,000 calories per 24 hours. (Page 281.) The basal heat production per kilogram of body weight was 13 calories per 24 hours. (Page 282.) Jap's surface area was 23.8 square meters. The basal 24-hour heat production per square meter of surface area was 2060 calories. (Page 286.) A "large" elephant produces the heat of about 30 men. (Page 268.)

BIBLIOGRAPHY

Bibliography on the Physiology of the Elephant

References given in this list are those dealing more particularly with the physiology of the elephant. The pages on which they are cited in this monograph are indicated in the author index. (See page 301.)

Allen, G. M. 1936. Zoological results of the George Vanderbilt African Expedition of 1934. Part II—The Forest Elephant of Africa. Proc. Acad. Nat. Sci., Phila., vol. 88, 15-44.

v. **Anghi**. 1934. Geburt in Budapest. Zool. Garten., Jhrg. 7 (N. F.), 68.

Antonius, O. 1932. Report from Munich Zoological Gardens of birth of Indian elephant. Zool. Garten, Jhrg. 5 (N. F.), 170.

Armandi, P. 1843. Histoire militaire des éléphants, depuis les temps les plus reculés jusqu'à l'introduction des armes à feu. Paris.

Benedict, F. G., E. L. **Fox**, and M. L. **Baker**. 1921. The surface temperature of the elephant, rhinoceros, and hippopotamus. Amer. Journ. Physiol., vol. 56, 464-474.

———, ———, and ——— 1921. The skin temperature of pachyderms. Proc. Nat. Acad. Sci., vol. 7, 154-156.

Brody, S., R. C. **Procter**, and U. S. **Ashworth**. 1934. Growth and development with special reference to domestic animals. XXXIV. Basal metabolism, endogenous nitrogen, creatinine and neutral sulphur excretions as functions of body weight. Univ. Missouri, Agric. Exper. Sta., Research Bull. 220.

———, and R. C. **Procter**. 1935. Growth and development with special reference to domestic animals. XXXV. Energetic efficiency of milk production and the influence of body weight thereon. Univ. Missouri, Agric. Exper. Sta., Research Bull. 222. Errata under Foreword.

Camper, P. 1802. Description anatomique d'un éléphant mâle. Publiée par son fils, A. G. Camper, Paris.

Chaney, R. W. 1935. The Kucha Flora in relation to the physical conditions in Central Asia during the late tertiary. Svenska Sällskapet för Antropologi och Geografi, Geografiska Annaler, Sven Hedin, Arg. XVII, 92.

——— 1935. The food of fossil elephants. Carnegie Inst. Wash. News Service Bull., vol. 3, 177.

Chapman, H. C. 1874-81. The placenta and generative apparatus of the elephant. Journ. Acad. Nat. Sci., Phila., vol. 8 (2d ser.), 413.

Colin, G. 1888. Traité de physiologie comparée des animaux, Paris, 3d ed., vol. 2, 476, 848, 849, and 854.

Corse, J. 1799. Observations on the manners, habits, and natural history of the elephant. Philos. Trans. Roy. Soc. London, Part I, 31-55.

——— 1799. Observations on the different species of Asiatic elephants and their mode of dentition. Philos. Trans. Roy. Soc. London, Part I, 205-236.

Digby, B. 1926. The mammoth and mammoth-hunting in North-East Siberia. New York.

Doremus, C. A. 1882. Analysis of elephant's milk. Med. News, Phila., vol. 40, 282.

Dover, C. 1932. Duration of life of some mammals. Journ. Bombay Nat. Hist. Soc., vol. 36, 244-245.

Evans, G. H. 1901 and 1910. Elephants and their diseases. Rangoon.

Flower, S. S. 1931. Contributions to our knowledge of the duration of life in vertebrate animals—V: Mammals. Proc. Zool. Soc. London, 190-197.

Forbes, A., S. **Cobb**, and McK. **Cattell**. 1921. An electrocardiogram and an electromyogram in an elephant. Amer. Jour. Physiol., vol. 55, 385-389.

Fourcroy, A. F., and L. N. **Vauquelin**. Journ. Soc. d. Pharm., Paris, vol. 1, 129. (Cited by D. J. C. Reil. 1800. Ueber die Benzoesäure im Harn grassfressender Thiere. Arch. f. d. Physiol., Halle, vol. 4, 162-164.)

Galen, C. 1550. Latin translation of Galen's works, Lyons, vol. 1, 295. (De Anatomicus administrationibus, Book 7.)

Giard, A. 1907. L'éléphant d'Afrique a-t-il une cavité pleurale? Compt. Rend. Acad. Sci., Paris, vol. 144, 306-308.

——— 1907. À quel moment et comment s'oblitèrent les cavités pleurales des éléphants? Compt. Rend. Acad. Sci., Paris, vol. 144, 471-474.

——— 1907. Nouvelles remarques sur l'oblitération de la cavité pleurale des éléphants. Compt. Rend. Acad. Sci., Paris, vol. 144, 1318-1320.

Gilchrist, W. 1851. A practical treatise on the treatment of the diseases of the elephant, camel, and horned cattle, with instructions for preserving their efficiency. Calcutta.

Gowers, W. 1931. Letter of Sir William Gowers on the gestation period of the African elephant (*Loxodonta africana*). Proc. Zool. Soc. London, 1207-1208.

Grabowsky. 1905. Der Futtermittelverbrauch im Zoologischen Garten zu Breslau im Jahre 1904. Zool. Garten, Jhrg. 16, 1.

Grimpe, G. 1933. Elefantengeburten in Nordamerikanischen Zoos und Zirkusmenagerien. Zool. Garten, Jhrg. 6 (N. F.), 196-197.

Hagenbeck, C. 1908. Von Tieren und Menschen. Erlebnisse und Erfahrungen. Berlin.

——— 1909. Beasts and men. Translated by H. S. R. Elliot and A. G. Thacker, London and New York, 202.

Hartenfels, Georg. Christoph. Petri ab. 1715. Elephantographia curiosa, seu Elephanti Descriptio, juxta methodum et leges imperialis academiæ Leopoldino-Carolinæ naturæ curiosorum adornata, multisque selectis observationibus physicis, medicis et jucundis historiis referta, cum figuris æneis. Erfordiæ, Typis Joh. Henrici Groschii. 284 pages.

——— 1723. Idem, Edit. altera auctior et emendatior, cui accessit ejusdem auctoris oratio panegyrica de Elephantis, nec non Justi Lipsii epistola de eodem argumento erudite conscripta. Lipsiæ et Erfordiæ. Typis Joh. Mich. Funckii. 284 et 20 pag.

Heller, E. 1933. Elephants in and out of the zoo. Bull. Wash. Park Zool. Soc., Milwaukee, vol. 4, No. 1. 18 pages.

Herbert, A. 1917. The elephant. New York, 206.

Hesse, R. 1928. Die Ohrmuscheln des Elefanten als Wärmeregulator. Zeitschr. f. wiss. Zool., vol. 132, 314-328.

Howe, A. J. 1879. The autopsy of an elephant. Eclectic Med. Journ., vol. 39, 252-259.

Hundley, G. 1934. Statistics of height increments of Indian calf elephants. Proc. Zool. Soc. London, 697-698.

Hvass, H. 1932. Von der indischen Elefantin Ellen und ihren drei in Gefangenschaft geborenen Jungen. Zool. Garten, Jhrg. 5 (N. F.), 191-199.

Kofoid, C. A. 1935. On two remarkable ciliate protozoa from the cæcum of the Indian elephant. Proc. Nat. Acad. Sci., vol. 21, 501-506.

Krumbiegel, J. 1933. Wie füttere ich gefangene Tiere? Akademische Verlagsgesellschaft, Leipzig, 17.

Mayer, C. 1847. Beiträge zur Anatomie des Elephanten und der übrigen Pachydermen. Nova Acta Phys.-Med. Acad. Caes. Leop., Halle, vol. 22, 30 et seq.

Merriam, J. C. 1935. Early Man in America. Report of XVI Geological Congress. Carnegie Inst. Wash., News Service Bull., vol. 3, 185-190.

Miall, L. C., and F. Greenwood. 1877-78. The anatomy of the Indian elephant, Part I, The muscles of the extremities. Journ. Anat. and Physiol., London, vol. 12, 261-287.

——— and ——— 1877-78. The anatomy of the Indian elephant, Part II, Muscles of the head and trunk. Journ. Anat. and Physiol., London, vol. 12, 384-400.

——— and ——— 1878-79. The anatomy of the Indian elephant, Part III, Alimentary canal and its appendages. Journ. Anat. and Physiol., London, vol. 13, 17 and 22.

——— and ——— 1878. Studies in Comparative Anatomy, No. II, Anatomy of the Indian elephant, London.

Mitchell, P. C. 1916. On the intestinal tract of mammals. Proc. Zool. Soc. London, 210-211.

Möbius, K. 1892. Die Behaarung des Mammuths und der lebenden Elephanten, vergleichend untersucht. Sitzungsb. d. königl. preuss. Akad. d. Wissensch., Berlin, 527-538.

Moulines, A. 1682. An anatomical account of the elephant accidently burnt in Dublin, on Fryday, June 17, in the year 1681, etc.

Noback, C. V. 1932. 36th Ann. Report, New York Zool. Soc., 58.

Osborn, H. F. Proboscidea. A monograph of the discovery, evolution, migration and extinction of the mastodonts and elephants of the world. In press.

——— 1935. The ancestral tree of the Proboscidea. Discovery, evolution, migration, and extinction over a 50,000,000 year period. Proc. Nat. Acad. Sci., vol. 21, 404-412.

Owen, R. 1868. On the anatomy of vertebrates. London, vol. 3, 457.

Pagenstecher, H. A. 1872. Der indisch. Elephant. Verhandlungen des naturhistorisch-medizinischer Vereins zu Heidelberg, vol. 6, 96.

Perrier, E. 1907. Autopsie de l'éléphant d'Afrique Sahib mort au Muséum le 29 janvier 1907. Compt. Rend. Acad. Sci. Paris, vol. 144, 236.

Phisalix, M. 1907. Autopsie de l'éléphant d'Afrique Sahib mort au Muséum le 29 janvier 1907. Compt. Rend. Acad. Sci. Paris, vol. 144, 281-282.

Pliny the Elder. Natural Histories, Book VIII.

Priemel, K. 1930. "Ipani," die portugiesisch-ostafricanische Elefantin des Frankfurter Zoo, Zool. Garten, Jhrg. 3, 241.

Pütter, A. 1918. Studien über physiologische Ähnlichkeit. Arch. f. d. ges. Physiol., vol. 172, 367-412 (tables 2 and 3, 379 and 396).

——— 1923. Zur Physiologie der Riesentiere. Zool. Jahrb., Abt. f. allg. Zool. u. Physiol., vol. 40, 217-240.

Richmond, R. D. 1932-33. Elephants—Age to which they live in captivity. Journ. Bombay Nat. Hist. Soc., vol. 36, 494-496.

Röse, C. 1894. Ueber den Zahnbau und Zahnwechsel von Elephas indicus, Schwalbe's Morphologische Arbeiten, Jena, vol. 3, 173.

Rubner, M. 1924. Aus dem Leben des Kaltblüters, I. Biochem. Zeitschr., vol. 148, 240.

Sanderson, G. P. 1879. Thirteen years among the wild beasts of India. London, 2d ed.

Schiött, J. 1905. Ein Elefant als Nordpolfahrer. Zool. Garten., Jhrg. 46, 10-12.

——— 1908. Geburt eines Elefanten im Zoologischen Garten zu Kopenhagen. Zool. Garten, Jhrg. 49, 133-136.

Schmidt, M. 1884. Die Wachstumsverhältnisse des indischen Elefanten. Zool. Garten, Jhrg. 25, 4-19.

Schneider, K. M. 1930. Einige Beobachtungen über das Geschlechtsleben des indischen Elefanten. Zool. Garten, Jhrg. 3 (N. F.), 305-314.

Schrempp, W. 1934. Betrachtungen über den wilden und den zahmen Elefanten unter besonderer Berücksichtigung der Fütterung und Haltung des letzteren. Dissert., Hannover.

Shaw, W. 1900. Castration of an elephant. Vet. Journ. London, N. S., vol. 2, 151-152.

Smith, F. 1890. The histology of the skin of the elephant. Journ. Anat. and Physiol., London, vol. 24, 493-503.

Steel, J. H. 1885. A manual of the diseases of the elephant and of his management and uses. Madras.

Stock, C. 1935. Exiled elephants of the Channel Islands, California. Scientific Monthly, Sept., 205-214.

Stricker, W. 1878. Zur Geschichte der Elephanten. Zool. Garten, Jhrg. 19, 380-382.

Stukeley, W. 1723. An essay towards the anatomy of the elephant, from one dissected at Fort St. George, Oct. 1715, and another at London, Oct. 1720. London, 89. (Reference inaccessible.)

Sunamoto, E. 1931-32. The elephant. Osaka. 2 volumes.

Takamatsu, M. 1935. Vergleichende Untersuchungen des Harns von verschiedenen Tieren und vom Menschen. Journ. Biochem., vol. 21, 427-433.

——— 1935. Organische Bestandteile des Elefantenharns. Journ. Biochem., vol. 21, 435-438.

Turpin. 1771. Histoire Universelle du Royaume de Siam. Paris, vol. 1, 265.

v. Vogel, H. A. 1817. Analyse des Urins vom Rhinoceros und vom Elephanten. Journ. f. Chemie u. Physik, vol. 19, 156-165.

Vulpian, A., and J. M. Philipeaux. 1856. Notes sur le coeur, le foie et les poumons d'un éléphant (femelle). Ann. d. Sci. Nat., 4th ser., Zool., vol. 5, 183-204.

Watson, M. 1874. Contributions to the anatomy of the Indian elephant (*Elephas indicus*), Part III, The head. Journ. Anat. and Physiol., London, vol. 8, 90.

Zipperlen, A. 1880. Telegram. Zool. Beobachter, Jhrg. 21, 96.

Supplementary Bibliography Dealing With the Elephant

In the collection of the voluminous and frequently obscure literature on the elephant we have been very much aided by Dr. Blanche B. Daly. The large majority of the citations were checked by consulting the original articles. A few were not available to us.

Adloff, P. 1919-20. Zur Ontogenie des Elefantengebisses. Anat. Anz., vol. 52, 534-540.

Allan, C. W. 1911-13. The birth of a wild elephant calf. Journ. Bombay Nat. Hist. Soc., vol. 21, 239-240.

Anderson, R. J. 1883. Anatomy of Indian elephant. Journ. Anat. and Physiol., vol. 27, 491-494.

de Beaux, O. 1912. Ueber einige Säugetiere in Carl Hagenbecks Tierpark in Stellingen. Zool. Anzeig., vol. 39, 561-575. (Characteristics and measurements of the Congo elephant, 566-570.)

Beckett, J. 1932-33. Death of elephant from rabies. Journ. Bombay Nat. Hist. Soc., vol. 36, 242-243.

Beddard, F. E. 1893. The brain of the African elephant. Proc. Zool. Soc. London, vol. 2, 311-315.

——— 1902. The birth of an elephant. Proc. Zool. Soc. London, vol. 2, 320-323.

——— 1909. Cambridge Natural History, Mammalia, vol. 10, 216-232. (Certified height of Jumbo given, viscera of elephant described.)

Blair, P. 1710. Osteographia Elephantina, or a full and exact description of all bones of an elephant, with their several dimensions, etc. Philos. Trans., vol. 27, 51-168.

——— 1718. A description of the organ of hearing in the elephant. Philos. Trans., vol. 30, 885-898.

Blunt, D. E. 1933. Elephant. London (East Africa). 260 pages, 22 illus. (Control, preservation, hunting.)

Boas, J. E. V. 1906. Fehlen der Pleurahöhlen beim indischen Elephanten. Morph. Jahrb., Leipzig, vol. 35, 494-495.

———, and S. Paulli. 1925. The elephant's head. Studies in the comparative anatomy of the organs of the head of the Indian elephant and other mammals. Jena, Second Part, with 31 plates.

Bolau, H. 1887. Der Elephant in Krieg und Frieden und seine Verwendung in unsern afrikanischen Kolonien. Hamburg. Samml. gemeinverständl. wissensch. Vorträge, N. F., 2d ser., vol. 6, 3-32.

Bopayyah, A. B. 1929. Natural diarrhea in elephants. Indian Veterin. Journ., vol. 5, 259-264.

Bor, N. L. 1927-28. Musth in elephant. Journ. Bombay Nat. Hist. Soc., vol. 32, 594-596.

Bostock, E. H. 1928. Menageries, circuses and theatres. New York, 305 pages.

Botar, J. 1931. Études anatomiques sur le système nerveux sympathique de l'éléphant des Indes. Bull. Mus. Hist. Nat. Paris, vol. 3 (2d ser.), 722-726.

Bregmann, L. E. 1915-16. Neue Untersuchungen zur Kenntnis der Pyramidenbahn. 2. Die Oblongatapyramide des Elephanten. Anat. Anz., vol. 48, 235-240.

Brehms Thierleben. 1877. Leipzig, vol. 3, 469-501. (General information on elephant.)

Bronn, H. G. 1874-1900. Klassen und Ordnungen des Thier-Reiches. Säugethiere. Mammalia, vol. 6, Abt. 5. (Anatomical facts concerning the elephant. Teeth, 109 and 1033.)

Brown, C. E. 1934. Captive pigmy elephants in America. Journ. Mammal., vol 15, 248-250.

Buck, A. H. 1887-90. A contribution to the anatomy of the elephant's ear. Trans. Amer. Otol. Soc., New Bedford, vol. 4.

——— 1887-90. A revised description of the anatomy of the elephant's ear. Trans. Amer. Otol. Soc., New Bedford, vol. 4, 15 pages.

Buddenbrock, W. von. 1928. Grundriss der vergleichenden Physiologie. Berlin. (Lungs, 354; heat regulation of elephant, 373; concentration of urine and blood, 703; pulse, 780.)

Buffon, G. L. L. de. 1800. Histoire naturelle, Paris, vol. 28, 89-282. (General account of the elephant.)

——— 1775. Oeuvres complètes, Paris, vol. 4, 187-316. (Sizes, ages, and diet of elephant; comparison with horse and with ruminants.)

Burne, R. H. 1902. Flexor carpi radialis of the elephant. Journ. Anat. and Physiol., vol. 37, July, lxii-lxiv.

Cabrera, A. 1927. Sobre el origen y significación del entrecruzamiento de las defensas en algunos elefantes. Biol. Soc. Españ. Hist. Nat., vol 27, 441-449.

Champion, F. W. 1927-28. Wild elephants in the United Provinces. Journ. Bombay Nat. Hist. Soc., vol. 32, 127-132, 4 photos.

——— 1928-29. On "natural deaths" in wild elephants. Journ. Bombay Nat. Hist. Soc., vol. 33, 433-434.

Chang, H. 1929. Die Funktion des Kauapparatus bei den Proboscidiern. Palæobiologica, vol. 2, 34-48.

Chapman, H. C. 1887. Notes on the anatomy of the Indian elephant. I: Some observations on the brain. Journ. Comp. Med. and Surg., vol. 8, 149-153.

Christy, C. 1924. Big game and Pygmies. London, 325 pages.

Cnyrim, E. 1914. Schläfendrüse und Lidapparate des Elefanten. Anat. Anz., Jena, vol. 46, 273-279.

Crisp, E. 1855. On the relative weight of the body and of the viscera of the elephant. Proc. Zool. Soc. London, vol. 23, 186-188.

Cunningham, D. J. 1882. Challenger Reports, vol. 5, part 16, 1-192. (Report on the Marsupialia; contains an account of the plantar muscle of the elephant foot, 104-106.)

Cuvier, G. 1806. Sur les éléphants vivants et fossiles. Ann. du Muséum d'histoire naturelle, vol. 8, 1-58, 93-155, and 249-269.

DÖNITZ, W. 1872. Ueber die Niere des afrikanischen Elefanten. Arch. f. Anat., 85-89.

DURAND, S. 1909. Rapports de la Plèvre avec la cage thoracique chez les vertébrés aériens. Bull. Soc. d'Histoire Nat. de Toulouse, vol. 42 (No. 2), 33-96. (Elephant, 64-74.)

DURRIEUX, A. 1912. Présentation d'un foetus d'éléphant. Compt. Rend. Soc. Biol., vol. 2, 188-189.

DUVAL, J. B. 1849. Anomalies des défenses de l'éléphant. Compt. Rend. Acad. Sci. Paris, vol. 29, 145-148.

——— 1850. Deuxième note sur l'anomalie des défenses de l'éléphant. Compt. Rend. Acad. Sci. Paris, vol. 30, 177-179.

EALES, N. B. 1925. External features, skin and temporal gland of a fœtal African elephant. Proc. Zool. Soc. London, part 2, 445-456.

——— 1926. The anatomy of the head of a foetal African elephant, *Elephas africanus (Loxodonta africana).* Trans. Roy. Soc. Edin., vol. 54, 491-551, 12 plates.

——— 1926. Einige Anmerkungen über die Monographie von Boas und Paulli (The elephant's head, Part 2, Jena, 1925). Anat. Anz., vol. 61, 361-365.

EDINGER, T. 1930. Kreisförmige Elefanten-Stosszähne. Natur. u. Museum, vol. 60, 45-47. (60. Ber. Senckenberg. Nat. Ges. Frankfurt a. M.)

——— 1932. Wie alt werden Säugetiere? Der Elephant Napoleons "Siam" der Hundertfünfzigjährige. Natur. u. Museum, vol. 62, 389-390. (Age statistics in captivity.)

EDWARDS, A. M. 1899. Les éléphants de la ménagerie du Muséum. Bull. Mus. Paris, vol. 5, 404-405.

EDWARDS, H. MILNE. 1857. Leçons sur la physiologie et l'anatomie comparée de l'homme et des animaux. Paris, vol. 1-14. (Elephant, structure of molar teeth, vol. 6, 160-161; mode of renewing teeth, vol. 6, 179-180; structure of trunk, vol. 11, 462; conformation of placenta, vol. 9, 558-560.)

EGGELING, H. 1901. Ueber die Schläfendrüse des Elephanten. Biol. Centralbl., Leipzig, vol. 21, 443-453.

ELWES, J. 1915-17. Altitude to which elephants ascend. Journ. Bombay Nat. Hist. Soc., vol. 24, 355.

FICK, L. 1844. Über das Labyrinth des Elephanten. Müllers. Archiv f. Anat., 431-432.

FILIPPI, FIL. DE. 1854. Über eigenthümliche Organe der Mundschleimhaut des Elephanten. Zeitschr. f. wiss. Zool., vol. 5, 26-28.

FORBES, W. H. 1879. On the anatomy of the African elephant. Proc. Roy. Soc. London, 420-435.

FOURCROY, A. F. 1803. Observations sur les calculs des animaux, comparés à ceux de l'homme. Ann. du Mus., Paris, vol. 2, 201-209. (Author states that many intestinal concretions or stones of the elephant are in the museum. These consisted almost exclusively of the triple phospate of ammonia and magnesium.)

FOX, H. 1923. Disease in captive wild animals and birds. Phila., 665 pages. (Actual weight of brain and the relation of this to that of the body in 196 animals; elephant, 393.)

FRADE, F. 1925. Os elefantes actuais e os seus antepassados. A propósitio de "Maputo" e de "Ipana." Lisboa, Soc. Sci. Nat. Port., 1-48, 10 figs. (Elephants past and present.)

GALEN, C. 1550. Articles on the elephant are given in the Index in Galen's works (Latin translation), Lyons, vol. 4.

GAUTIER, G. A. 1820. Examen de la trompe d'un éléphant. Journ. de Phys., vol. 90, 421-423.

——— 1820. Über die Haut des Elephantenrüssels. Meckels deutsch. Arch. f. Physiol., vol. 6, 477-479.

GOODWIN, G. G. 1925. The first living elephant in America. Journ. Mammal., Baltimore, vol. 6, 256-263, 3 plates.

GRATIOLET, P. 1855. Sur l'encéphale de l'éléphant. Compt. Rend. Acad. Sci. Paris, vol. 40, 1053-1055.

HARPER AND BROS. 1844. The elephant as he exists in a wild state and as he has been made subservient, in peace and war, to the purposes of man. Published by Harper and Bros., New York. (A popular treatment of the elephant, with especial emphasis upon historical and classical literature, replete with anecdotes but contains few statements of scientific value.) 300 pages.

HARRISON, R. 1850. On the larynx, trachea and œsophagus of the elephant. Proc. Irish Acad., vol. 4, 132-135.

——— 1850. On the anatomy of the lachrymal apparatus in the elephant. Proc. Irish Acad., vol. 4, 158-165.

Heller, E. 1934. Nature's most amazing mammal (elephant). Nation. Geogr. Mag., vol. 65, 729-759.

Hilzheimer, M. 1912. Das Mammut. Die allmählich wachsende Kenntnis von seinem Aussehen. Mit. e. Reconstruktionsversuch. Natur, Leipzig, 398-403, 413-417. (Primigenesic legends and reconstruction.)

Home, E. 1799. Some observations on the structure of the teeth of graminivorous quadrupeds, particularly those of the elephant and *sus Æthiopicus.* Philos. Trans., vol. 89, 237-258.

——— 1823. On the difference of structure between the human Membrana Tympani and that of the elephant. Philos. Trans., 23-26.

Houel, J. P. L. L. 1803. Histoire naturelle des deux Éléphants, mâle et femelle, du Muséum de Paris. Paris, 4to. (External parts only. These were the animals afterwards dissected by Cuvier.)

Hubbard, W. D. 1928. Observations on the elephants of northern Rhodesia and Portugese East Africa. Journ. Mammal., vol. 9, 39-43.

Huxley, T. H. 1864. Lectures on the elements of comparative anatomy. London. (Contains an account of a foetal elephant skull, 262-264.)

Jammes, L., and S. Durand. 1909. Nouvelles observations sur l'appareil respiratoire de l'éléphant. Bull. Soc. d'Histoire Nat. de Toulouse, vol. 42, 169-174.

Kelley, F. B. 1931. The land of sawdust and spangles—a world in miniature. Nation. Geogr. Mag., October, vol. 60. (Notes with regard to circus elephants and the date of arrival of the first pachyderm in this country, 467-470, and 471.)

v. Kolmer, W. 1921. Über die Tastorgane von *Elephas indicus.* Anat. Anz. vol. 54, 73-77.

Kunz, G. F. 1916. Ivory and the elephant. New York, 3-527. (Chapter entitled "Elephants historical" on 136-191; Egyptian, Chinese, Buddhist, Greek, and Roman records of elephants; describes offensive and defensive armour of Indian war elephant; mentions Jumbo and other elephants in America.)

Leeuwenhoek, A. van. 1712. Some remarks upon the disposition of the parts and microscopical observations upon the contexture of the skin of elephants. Philos. Trans., vol. 27, 518-522.

Lucas, F. A. 1923. How elephants are mounted. A chapter in the history of taxidermy. Journ. Amer. Mus. Nat. Hist., vol. 23, 597-605.

Lydekker, R. 1907. The ears as a race-character in the African elephant. Proc. Zool. Soc. London, 380-403. (19 illustrations of ear of African elephant; discussion of the shape, size, and measurements of the ear; records of heights of elephants.)

——— 1907. Local variation in the African elephant. Knowledge and Scientific News, London, vol. 4, 267-270. (Heights of elephants.)

——— 1914. The Malay race of the Indian elephant. Proc. Zool. Soc. London, 285-288.

Menon, P. G. 1926. Elephants and their care. Indian Forester Dehra Dun, vol. 52, 5-14. (Care of elephant in captivity.)

Mills, E. C. 1919. Interesting specimen; skull of Ringling Brothers' largest elephant. Dental Summary, Toledo, vol. 39, 459-460. (Life history of elephant that died in Columbus during exhibition of Ringling Brothers' Circus in 1918.)

Milroy, A. J. M. 1922. A short treatise on the management of elephants. Shillong, Gov't Press, 69 pages, 10 photos.

Mitchell, P. C. 1911. On longevity and relative viability in mammals and birds, with a note on a theory of longevity. Proc. Zool. Soc. London, 425-548. (Longevity of elephant discussed, 452.)

Mojsisovics, A. von. 1879. Zur Kenntnis des afrikanischen Elephanten. Berlin, Archiv f. Naturg., vol. 45, 56-92. (Anatomy of elephant.)

——— 1883. Nachträge zur Anatomie von *Loxodon africanus.* Steiermark, Mittheil., 171-192. (Deals chiefly with the pleural cavity.)

Mooney, H. F. 1928-29. Some observations on wild elephants in Orissa. Journ. Bombay Nat. Hist. Soc., vol. 33, 430-433. (Map.)

Morris, R. C. 1927-28. On "natural deaths" in wild elephants. Journ. Bombay Nat. Hist. Soc., vol. 32, 794-795.

——— 1931-32. Unerupted tusks of elephants. Journ. Bombay Nat. Hist. Soc., vol. 35, 889-891.

——— 1932-33. Elephants eating earth. Journ. Bombay Nat. Hist. Soc., vol. 36, 496-497.

Mouquet, A. 1922. Contractions musculaires cloniques chez l'éléphant. Bull. Mus. Hist. Nat., Paris, vol. 28, 35-37.

——— 1929. Hasdrubal et l'énucage des éléphants. Bull. Acad. Vétér. France, vol. 2, 78-80.

Müller, R. J. 1929. Die Überführung der Elefanten von Urana in den zoologischen Garten Sofia. Zool. Garten, Jhrg. 1 (N. F.), 411-416.

Neuville, H. 1923. Sur la glande iléocaecale des Éléphants. Bull. Mus. Hist. Nat., Paris, vol. 29, 198-204.

Osborn, H. F. 1921. Heads of African elephants. Journ. Amer. Mus. Nat. Hist., New York, vol. 21, 244-245.

Owen, R. 1857. Description of the fœtal membranes and placenta of the elephant (*Elephas indicus*, Cuv.), with remarks on the value of placentary characters in the classification of the mammalia. Philos. Trans., vol. 147, 347-353.

——— 1840-45. Odontography, or a treatise on the comparative anatomy of the teeth. London, vol. 1, 1-655. (Elephant, 625-655; Mastodon, 613-624, Transitional Mastodon, 624.)

Perrault, Cl. 1734. *Mémoires de l'Académie Royale des Sciences*, vol. 3, (Pt. 3), 161.

——— 1758. Describes the African elephant in *Mémoires pour servir à l'Histoire Naturelle des Animaux*, Amsterdam, vol. 2.

Pettit, A. 1907. Sur le rein de l'éléphant d'Afrique. Arch. Zool. Paris, vol. 7 (ser. 4), ciii-cxi.

——— 1907. Sur la musculature de l'éléphant d'Afrique. Bull. Muséum Paris, vol. 13, 235-237.

——— 1908. Sur le rein de l'éléphant d'Asie (*Elephas indicus*). Compt. Rend. Soc. Biol. Paris, vol. 1, 326-327.

Pocock, R. I. 1916. On the scent-glands in mammals. Proc. Zool. Soc. London, 742-755. (Description and illustrations of the temporal gland in elephant, 750-755.)

Pohle, H. 1926. Notizen über afrikanische Elephanten. Zeitschr. Säugertierkunde, Berlin, vol. 1, 58-64. (Type and locality of African elephant.)

Reade, L. L. 1931-32. Rogue elephants in the Khasi hills. Journ. Bombay Nat. Hist. Soc., vol. 35, 674-675.

Retterer, E. 1926. Structure de la défense d'éléphant. Compt. Rend. Soc. Biol., Paris, vol. 1, 255-259.

Retzer, R. 1912. The anatomy of the heart of the Indian elephant. Anat. Rec., vol. 6, 75-90.

Richards, H. 1887-90. A further report on the anatomy of the elephant's ear. Trans. Amer. Otol. Soc., New Bedford, vol. 4, 587-604.

——— 1891-93. A concluding report on the anatomy of the elephant's ear. Trans. Amer. Otol. Soc., New Bedford, vol. 5, 139-148.

Ruge, G. 1906. Form des Brustkorbes und Lagerung der Lungen im Brustkorbe beim indischen Elefanten. Morph. Jahrb., Leipzig, vol. 35, 496-505.

Salensky, W. 1903. Zur Phylogenie der Elephantiden. Biol. Centralbl., Leipzig, vol. 23, 793-803.

Schenke, H. 1926. Das Euter des afrikanischen Elefanten. Zeitschr. ges. Anat., vol. 81, 412-419. (Weitgehende Verwandtschaft mit der menschlichen Milchdrüse.)

Schmidt, M. 1882. Die Krankheiten der Elephanten. Zool. Garten, Jhrg. 23, 234-236.

Schönberg, F. 1930. Über den mikroskopischen Bau der Elefantenhaut. Zeitschr. Säugetierkunde, vol. 5, 9.

Schouteden, H. 1911. L'éléphant nain du Congo. (Musée du Congo Belge, Tervueren.) Revue Zool. Africaine, vol. 1, 222-229. (This article discusses chiefly *Elephas pumilio*.)

Schultz, C. H. 1839. Sur le sang de l'éléphant. Compt. Rend. Acad. Sci. Paris, vol. 8, 136.

——— 1839. Ueber das Elephantenblut. Muellers Arch. f. Anat., 252-254.

Schuster, L. 1929. Wie stillt der Elefant während der Trockenzeit in den Steppengebieten sein Wasserbedürfnis? Zool. Garten, Leipzig, Jhrg. 1 (N.F.), 302-304.

Seba, A. 1734. Locupletissimi rerum naturalium Thesauri accurata descriptio. Amst., vol. 1, 175 (African elephant fœtus).

Shurtleff, N. B. 1846. On some peculiarities of the skeleton of *Elephas indicus*. Proc. Boston Soc. Nat. Hist., vol. 2, 116-118.

Slade, H. 1903. On the mode of copulation of the Indian Elephant. Proc. Zool. Soc. London, 111-113.

Sokolowsky, A. 1916. Die Nahrung der Elefanten. Deutsche tierärztl. Wochenschr., Hannov., vol. 24, 14-17. (From the Zoological Garden in Hamburg, Germany. Food habits of captive elephants in zoological parks.)

Stockley, C. H. 1922. Notes on Lydekker's "Game-animals of India." Journ. Bombay Nat. Hist. Soc., vol. 28, 529-533. (Field notes and measurements of Indian game animals.)

Steinhardt, J. von. 1922. Vom Elefanten. Neue biologische Forschungsergebnisse und Beobachtungen aus freier Wildbahn. Verh. Nat. Ver. Hamburg, vol. 29, 27-28.

Stukeley, W. 1733. On the spleen and anatomy of an elephant. London, fol.

SUPLY. 1715. Remarques anatomiques sur un éléphant ouvert au fort Saint-Georges.

TENNENT, J. E. 1861. Sketches of the natural history of Ceylon with narratives and anecdotes illustrative of the habits and instincts of the Mammalia, birds, reptiles, fishes, insects, etc., including a monograph of the elephant and a description of the modes of capturing and training it. London, 75-240. (Special emphasis upon the Ceylon elephant.)

TODD, W. 1913. Notes on the respiratory system of the elephant. Anat. Anz., Jena, vol. 44, 175-183.

TURNER, W. 1876. Lectures on the comparative anatomy of the placenta, 1st series, Edinburgh. (Relates some observations on the structure of the placenta in the elephant.)

TUTEIN-NOLTHENIUS, A. C. 1935. Birth of an elephant calf *(Elephas maximus).* Journ. Bombay Nat. Hist. Soc., vol. 38, 183-184.

VIRCHOW, H. 1903. Über den Orbitalinhalt des Elefanten. Sitzber. Ges. natf. Freunde, Berlin, 341-354.

——— 1905. Weitere Bermerkungen über den Lidapparat des Elefanten. Sitzber. Ges. natf. Freunde, Berlin, 189-194.

——— 1910. Hand und Fuss des Elephanten nach Form zusammengesetzt. Sitzber. Ges. natf. Freunde, Berlin, 77-87.

——— 1910. Ueber die sagittal-flexorische Bewegung im Hinterhauptsgelenke des Elefanten. Sitzber. Ges. natf. Freunde, Berlin, 131-135.

——— 1910. Ueber einen Fugenknochen im Epistropheus des Elefanten. Sitzber. Ges. natf. Freunde, Berlin, 251-253.

WATSON, M. 1872. Contributions to the anatomy of the Indian elephant, Part I. Journ. Anat, and Physiol., vol. 6, 82-94.

——— 1873. Contributions to the anatomy of the Indian elephant, Part II. Journ. Anat. and Physiol., vol. 7, 60-74.

——— 1874. Contributions to the anatomy of the Indian elephant, Part III. Journ. Anat. and Physiol., vol. 8, 85-94.

——— 1875. Contributions to the anatomy of the Indian elephant, Part IV. Journ. Anat. and Physiol., vol. 9, 118-133.

WEBER, M. 1927. Die Saügetiere, Einführung in die Anatomie und Systematik der recenten und fossilen Mammalia. Jena, 2d ed., vol. 1, Anat. Teil, 303 (Elephant).

WETTSTEIN, O. 1920. Äussere morphologische Unterschiede zwischen Feten von *Elephas africanus* und *E. maximus.* Arkiv Zool. Stockholm, vol. 13, No. 15, 15 pages.

WIEGMANN, A. F. A. 1839. Begattung des Elefanten. Archiv f. Naturg., Jhrg. 5, vol. 1, 110.

WINDLE, B. C. A. 1901. On the muscles of the Ungulata. Proc. Zool. Soc. London, vol. 2, 656-704. (Elephant mentioned.)

——— and F. G. PARSONS. 1903. On the muscles of the Ungulata. Proc. Zool. Soc. London, vol. 2, 261-298. (Elephant mentioned.)

WINTERSTEIN, H. 1925. Handbuch der vergleichenden Physiologie. Jena, vol. 1 (Pt. 1). (Elephant, 1193 and 1208; blood, size of corpuscles, etc.)

——— 1921. Handbuch der vergleichenden Physiologie. Jena, vol. 1 (Pt. 2). (Elephant respiration, 952, 955, 963, and 965.)

——— 1911. Handbuch der vergleichenden Physiologie. Jena, vol. 2 (Pt. 1). (Chewing movements, 1123 and 1128; trunk, 1155.)

——— 1924. Handbuch der vergleichenden Physiologie. Jena, vol. 2 (Pt. 2). (Skin glands, 235.)

——— 1914. Handbuch der vergleichenden Physiologie. Jena, vol. 3 (Pt. 1). (Movements of the trunk, 92 and 155; glottis, 283.)

ZIMMER, H. 1929. Spiel um den Elefanten. Ein Buch von indischer Natur. München and Berlin, 192 pages.

ZIMMERMAN, E. A. W. 1783. Beschreibung und Abbildung eines ungebornen Elephanten. Erlangen.

ZUKOWSKY, L. 1924. Beitrag zur Kenntnis der Säugetiere der nördlichen Teile Deutsch-Südwest-Afrikas unter besonderer Berücksichtigung des Grosswildes. Arch. Natg. Berlin, vol. 90, 29-164. (*Loxodonta africana* field-notes on the race of S. W. Afr. Protect., 68.)

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